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Seattle, Washington

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NATIONAL MARINE FISHERIES SERVICE

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DEVELOPMENT AND OCCURRENCE OF LARVAE AND JUVENILES OF THE ROCKFISHES *SEBASTES CRAMERI*, *SEBASTES PINNIGER*, AND *SEBASTES HELVOMACULATUS* (FAMILY SCORPAENIDAE) OFF OREGON[1]

SALLY L. RICHARDSON[2] AND WAYNE A. LAROCHE[3]

ABSTRACT

Developmental series of larvae and juveniles of three species of northeast Pacific rockfishes (Scorpaenidae: *Sebastes*) are illustrated and described: *S. crameri* (8.0 to 130.5 mm standard length), *S. pinniger* (7.8 to 181 mm standard length), and *S. helvomaculatus* (7.7 to 183 mm standard length). The descriptions include a literature review, characters used for identification including meristics and supraocular spine patterns, distinguishing features, general development, morphology, fin development, spination, scale formation, and pigmentation. Occurrence in waters off Oregon is discussed.

The approach that was used to identify larval and juvenile specimens of *Sebastes* from plankton, midwater trawl, and bottom trawl collections from Oregon waters is presented, since 36 species reportedly occur there. Developmental terminology is newly defined for *Sebastes*. Larval and juvenile spination is presented schematically and defined.

Larvae and juveniles of the three species described here are compared with other known *Sebastes* larvae and juveniles from the northeast Pacific.

Data gathered during this study extend the southern range limit of *Sebastes emphaeus* to Punta Gordo, Calif.

Rockfish of the genus *Sebastes* are an important group of fishes in the northeast Pacific both in terms of number of species and in commercial and sport fisheries. Sixty-nine species of *Sebastes* occur between the Gulf of California and the Gulf of Alaska (Chen 1971, 1975). In 1975, Pacific trawl landings of *Sebastes* spp. in the United States and Canada, categorized as "Pacific ocean perch" and "other rockfish," were 17,400 metric tons (t) or 23.9% of the total trawl landings (Verhoeven 1976). In California, rockfish compose half the number of sportfish caught (Young 1969).

"Pacific ocean perch" (primarily *Sebastes alutus*) trawl landings in the United States and Canada declined from a peak of 14,000 t in 1965 to 8,500 t in 1975 and "other rockfish" landings subsequently increased from 8,600 t in 1965 to 16,300 t in 1973 and 13,300 t in 1975 (Pacific Marine Fisheries Commission 1964-76; Verhoeven 1976). Because of this shift in composition of trawl landings, knowledge of the biology of the individual species involved, including their early life history, is becoming increasingly important. Such information is relatively scarce, partly because of the difficulty involved in identifying the young stages.

Rockfish larvae, which are extruded live from ovoviviparous females, are pelagic as are young juveniles. The pelagic larvae are very abundant, ranking third or fourth in annual larval fish abundance off California (Ahlstrom 1961, 1965) and second only to osmerid larvae off Oregon (Richardson 1977; Richardson and Pearcy 1977). Juveniles are important as forage items for larger fishes, such as albacore (Powell et al. 1952) and salmon (Whitney 1893; Silliman 1941; Pritchard and Tester 1944; Merkel 1957), and marine birds (Follett and Ainley 1976).

Pelagic larvae and juveniles of relatively few of the 69 northeast Pacific rockfish species have been described. Illustrations or partial descriptions of pigment patterns have been presented for preextrusion or newborn larvae of 47 of these species but only 26 of these were reared to the point of yolk absorption (Table 1). The first larval developmental series of *Sebastes* spp. were presented as two unnamed species (Ahlstrom 1965) the second of

[1]From a final report for NOAA NMFS Contract No. 03-6-208-35343 submitted to Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, on 15 June 1977.

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which is now known to be *S. paucispinis* (Moser 1967; Moser et al. 1977). Complete development series from newly hatched larvae to benthic juveniles have only been described for *S. cortezi*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, *S. paucispinis*, and *Sebastes* sp. — Gulf of California Type A (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978).

This paper is a contribution to the knowledge of the early life history of northeast Pacific rockfishes. Developmental series of three species, *S. crameri*, *S. pinniger*, and *S. helvomaculatus*, are described for the first time. The first two species are important contributors to Oregon trawl landings (Niska 1976). Information on occurrence of larvae and juveniles of these three species off Oregon is also given. Because of the large species complex of *Sebastes* in the northeast Pacific and the difficulty in identifying young rockfish, e.g., adult keys cannot be used, the approach that was used to identify the specimens in this study is presented as part of the methodology.

MATERIALS AND METHODS

Collections

Specimens described in this paper came from collections in the School of Oceanography, Oregon State University. The collections were obtained with 70 cm bongo nets, neuston nets, meter nets, Isaacs-Kidd midwater trawls, beam trawls, and otter trawls off the Oregon coast since 1961 during all months of the year. Samples were taken along the entire coast, but were concentrated along an east-west transect off Newport, Oreg. (lat. 44°39.1′ N). All material had been preserved in either 5 or 10% Formalin[4] and most had been transferred to 30 or 40% isopropyl alcohol. Over 12,000 *Sebastes* larvae and juveniles were sorted from the available collections.

Approach to Identification

Geographic ranges of all known northeast Pacific species [excluding the new species being described by Lea and Fitch (Chen 1975), presumably from California] were recorded from the literature (Appendix Table 1). Additional range information gathered during this study extends the southern range of *S. emphaeus* through Oregon to Punta Gordo, Calif. (lat. 40°12.9′ N, long. 124°23.7′ W, depth 97 m). Adults of only 36 of these species are reported to occur off Oregon. The occurrence of two of these, *S. eos* and *S. rosaceus*, is questionable north of northern California (Chen 1971). Although ocean currents could potentially carry larvae and juveniles of additional species into Oregon waters, it is unlikely that large numbers of young of other species would be taken in an area where the adults do not occur. Following this assumption, tables of morphological characters were prepared for these 36 potential species. The most useful characters for identifying young rockfish were shape of the upper profile of the head (interorbital space) and presence or absence of specific head spines, particularly the supraocular (Appendix Table 2); number, including range and usual (most commonly occurring) number of dorsal fin rays, anal fin rays, and pectoral fin rays (Appendix Table 3); total number of gill rakers on the first gill arch (Appendix Table 4); number of lateral line pores (Appendix Table 5); number of diagonal scale rows below the lateral line (Appendix Table 6). Proportions of body parts related to standard length such as length of upper jaw, head length, length of longest dorsal spine, and body depth at pelvic fin insertion were compiled but were not particularly useful. Additional information which was sometimes helpful included records from trawl surveys off Oregon (Demory et al. 1976) and commercial catch trends in Oregon (Niska 1976) which gave indications of species common in trawlable habitats in the area. Pigment banding patterns of adults were also useful.

Initially, counts were made on each juvenile to be identified along with notes on additional, potentially useful characters. Data for each specimen were then screened through each of the appendix tables, and the species which did not agree were eliminated as potential candidates. This approach, together with some additional data from the literature as noted in the text, lead to positive identification for the species included in this paper.

Developmental series were established backwards from juveniles primarily on the basis of pigmentation, particularly that of the pectoral and pelvic fins and that on the dorsal and ventral body margins, general body shape (e.g., short and stubby, slender and elongate), and constancy in number of dorsal, anal, and pectoral fin rays which could be counted back to postflexion, sometimes

[4]References to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

flexion, larvae. Developmental series could not be carried back to newly extruded larvae in the plankton samples with certainty. Pigmentation is the primary character used to distinguish small larvae prior to development of fin rays and head spines. Pigment patterns of newborn larvae are often similar among a number of species and these patterns may change considerably by the time the yolk is absorbed (Westrheim 1975; Moser et al. 1977). Preextrusion and newborn larvae have been described for 29 of the 36 species of *Sebastes* off Oregon, but larvae reared to yolk absorption have only been described for 15 (Table 1). The number of species which have patterns similar to those that have been described is unknown. Rearing larvae of the remaining species to yolk absorption will be necessary to provide an adequate foundation for identification of small larvae in plankton samples. We had no opportunity to rear larvae from known parents.

Meristics[5]

Counts were made on unstained material as not enough specimens were available to make complete stained series for developmental ossification studies. [One to several pelagic juveniles of *S. crameri*, *S. pinniger*, and *S. helvomaculatus* were stained with alizarin red S (Taylor 1967) for examination of general bone structure, spination, and secondary caudal rays.] Fin spines and rays were only counted when they appeared to be fully formed structures under magnification, which may approximate initial ossification. Bases of fin rays, visible prior to actual ray formation, were not counted. In *Sebastes*, the 13th dorsal spine and the 3d anal spine form first as soft rays which then transform to spines beginning at the basal portion and continuing distally. These were considered to be "prespines" until spine formation was complete.

Counts were made of dorsal fin spines and rays, anal fin spines and rays, pectoral fin rays, pelvic fin rays, principal caudal fin rays, gill rakers on the upper and lower limb of the first gill arch, lateral line pores, and diagonal scale rows below the lateral line. In some cases Inda ink was applied to the right side of a fish to increase visibility of the latter two features.

[5]The term "meristic" is used here to refer to all countable characters.

Morphometrics

Measurements of various body parts of selected specimens were made to the nearest 10th or 100th of a millimeter using an ocular micrometer in a stereomicroscope as follows:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of hindgut at anus.

Head length (HL) = snout tip to cleithrum until no longer visible, then to posteriormost margin of opercle (SL of 30.3 mm on *S. crameri*, 16.8 mm on *S. pinniger*, 41.6 mm on *S. helvomaculatus*).

Snout length = snout tip to anterior margin of orbit of left eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest diameter of left orbit.

Interorbital distance = distance between dorsal margins of orbits.

Body depth at pectoral fin base = vertical distance from dorsal to ventral body margin at base of pectoral fin.

Body depth at anus = vertical distance from dorsal to ventral body margin immediately posterior to anus.

Pectoral fin length = distance from base to tip of longest ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic spine length = distance from base to tip of pelvic spine.

Pelvic fin length = distance from base to tip of longest ray.

Snout to origin of pelvic fin = distance along body midline to vertical through insertion of pelvic fin.

Parietal spine length = distance along posterior margin of parietal spine from insertion to tip.

Nuchal spine length = distance along posterior margin of nuchal spine from insertion to tip.

Preopercular spine length (third spine, posterior series) = distance from tip to basal insertion if visible, or to a line connecting the points of deepest indentation between preopercular spines 2 and 3 and spines 3 and 4 (posterior series).

Length of angle gill raker = distance from tip of gill raker to point of articulation with gill arch.

TABLE 1.—Summary of data on preextrusion larvae (P) or newborn, reared larvae (L) of northeast Pacific species of *Sebastes*. Asterisk indicates figure is included.

Species	Source															
	Eigenmann (1892)	Wales (1952)	Morris (1956)	DeLacy et al. (1964)	Ahlstrom (1965)	Moser (1967)	Waldron (1968)	Westrheim et al. (text footnote 7)	Westrheim et al. (text footnote 9)	Efremenko and Lisovenko (1970)	Harling et al. (text footnote 10)	Moser (1972)	Westrheim (1975)	Moser et al. (1977)	Moser and Ahlstrom (1978)	
S. aleutianus								P*		P*			P			
S. alutus				P*				P*		P*			P			
S. atrovirens																
S. auriculatus	(P*)			P*									P	L*		
S. aurora																
S. babcocki				[1]P*				[1]P*		[1]P*			P			
S. borealis																
S. brevispinis				P*						P*			P	P		
S. carnatus						L*								L*		
S. caurinus				P*									P	L*		
S. chlorostictus						L*								L*		
S. chrysomelas																
S. ciliatus											P*		P			
S. constellatus						L*								L*		
S. cortezi																
S. crameri								P*					P			
S. dalli						L*								L*		
S. diploproa				P*					P*				P	P		
S. elongatus						L*			P*				P	L*		
S. emphaeus																
S. ensifer						[2]L*								L*		
S. entomelas											P*		P			
S. eos						L*								L*		
S. exsul																
S. flavidus				P*									P	P		
S. gilli														L*		
S. goodei			L*										P	L*		
S. helvomaculatus									P*				P			
S. hopkinsi						L*								L*		
S. jordani			L*										P	L*		
S. lentiginosus																
S. levis						L*								L*		
S. macdonaldi						L*						L*		L*		
S. maliger				P*					P*				P	P		
S. melanops																
S. melanostomus														L*	L*	
S. miniatus														L*		
S. mystinus		P*							P*							
S. nebulosus																
S. nigrocinctus																
S. notius																
S. ovalis						L*								L*		
S. paucispinis			L*		L*	L*							P	L*		
S. peduncularis																
S. phillipsi																
S. pinniger							L*						P	L*		
S. polyspinis																
S. proriger									P*				P			
S. rastrelliger																
S. reedi								P*					P			
S. rosaceus						L*								L*		
S. rosenblatti														L*		
S. ruberrimus				P*					P*		P*		P			
S. rubrivinctus	P			([3])				([3])		([3])						
S. rufinanus																
S. rufus														P		
S. saxicola			L*					P*					P	L*		
S. semicinctus						L*								L*		
S. serranoides														P		
S. serriceps														L*		
S. simulator																
S. sinensis																
S. spinorbis																
S. umbrosus						L*								L*		
S. variegatus											P*		P			
S. varispinis																
S. wilsoni														P		
S. zacentrus									P*	P*	P*		P			
S. new sp. (Lea and Fitch)																

[1]Described as *S. rubrivinctus*, but northern occurrence indicates it must be *S. babcocki*.
[2]Described as *S. rhodochloris*.
[3]These descriptions of *S. rubrivinctus* must be *S. babcocki* due to the northern occurrence of specimens.

Longest dorsal fin spine = distance from base to tip.

Longest dorsal fin ray = distance from base to tip.

Longest anal fin spine = distance from base to tip.

All body lengths given refer to standard length unless noted otherwise.

Developmental Terminology

Terminology for development of *Sebastes* spp. used in this paper is as follows:

Preflexion larva = prior to notochord flexion.

Flexion larva = undergoing notochord flexion from time urostyle begins to slant upward until urostyle is in final upturned position and caudal fin is formed.

Postflexion larva = from completion of notochord flexion (urostyle may still extend beyond the base of the caudal fin) to onset of transformation of 13th dorsal spine and 3d anal spine from soft ray to spine, and to the associated onset of development of juvenile pigment pattern (usually addition of pigment to the dorsum).

Transforming larva = from onset to completion of transformation of 13th dorsal spine and 3d anal spine from soft ray to fully developed spine. Also from the onset of development of juvenile pigment pattern to development of distinctive juvenile pigmentation, often in the form of melanistic saddles over the dorsum.

Pelagic juvenile = from completion of formation of 13th dorsal and 3d anal spine (and thus attainment of adult complement of actual fin spines and rays) and development of juvenile pigmentation until no longer captured pelagically.

Benthic juvenile = from time of first capture on bottom and usual associated decrease in intensity of melanistic pigmentation to attainment of sexual maturity.

Spination (Figure 1, Table 2)

Difficulties arise in naming all the spines found in the head region of larvae and juveniles of *Sebastes* because not all are found in adults. Further complications arise because the names traditionally used for a number of the head spines do not reflect the bone from which the spine originates. For these reasons we include a composite diagram of spines which may occur during the larval and juvenile periods. The terminology is a combination and modification of that used by Phillips (1957), Chen (1971), Moser (1972), and Moser and Ahlstrom (1978). Most names used in this paper are the same as those used for adult rockfishes to avoid confusion, even though the bones from which the spines originate are not indicated by the name. Exceptions are as follows. The two spines found on the opercular margin are here called the subopercular and the interopercular according to the bones from which they originate. The superior posttemporal (supracleithral of adults), inferior posttemporal (not found in adults), and supracleithral (cleithral of adults) are so-called because of their origin. This is done to avoid confusion with a spine present on the posterior margin of the cleithrum, which is here called the cleithral spine. Use of the term infraorbital

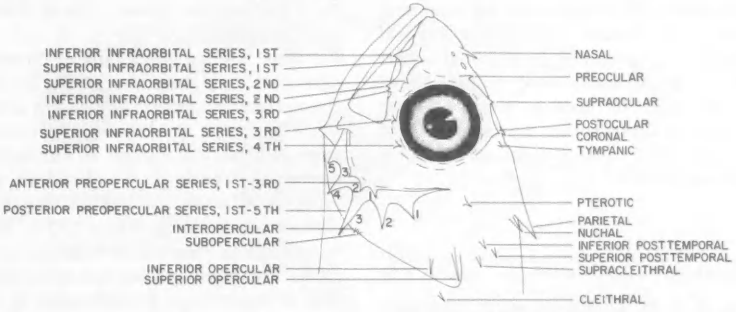

FIGURE 1.—Composite diagram of spines present in the head region of larval and juvenile *Sebastes* species including names used in this paper. Refer to Table 2 for corresponding names used for adults and bones from which spines originate.

TABLE 2.—Names of head region spines of larval and juvenile *Sebastes* spp. used in this paper with corresponding names used for adults and bones from which the spines originate. Spines listed in the first column are shown in Figure 1 clockwise beginning with the nasal.

Name used in this paper	Name used in adults[1]	Bone from which spine(s) originates[2]
Nasal	Nasal	Nasal
Preocular	Preocular	Prefrontal
Supraocular	Supraocular	Frontal
Postocular	Postocular	Frontal
Coronal	Coronal	Frontal
Tympanic	Tympanic	Frontal
Pterotic	Pterotic	Pterotic
Parietal	Parietal	Parietal
Nuchal	Nuchal	Parietal
Inferior posttemporal	—	Posttemporal
Superior posttemporal	Supracleithral	Posttemporal
Supracleithral	Cleithral	Supracleithrum
Cleithral	—	Cleithrum
Superior opercular	Opercular	Opercle
Inferior opercular	Opercular	Opercle
Subopercular	Gill cover spine	Subopercle
Interopercular	Gill cover spine	Interopercle
Posterior preopercular series, 1st-5th	Preopercular	Preopercle
Anterior preopercular series, 1st-3d	—	Preopercle
Superior infraorbital series, 4th	—	Infraorbital 3 (2d suborbital)
Superior infraorbital series	—	Infraorbital 2 (1st suborbital)
Inferior infraorbital series, 3d	—	Infraorbital 1 (preorbital)
Inferior infraorbital series, 2d	Lachrymal projection (suborbital spine)	Infraorbital 1 (preorbital)
Superior infraorbital series, 2d	—	Infraorbital 1 (preorbital)
Superior infraorbital series, 1st	—	Infraorbital 1 (preorbital)
Inferior infraorbital series, 1st	Lachrymal projection (suborbial spine)	Infraorbital 1 (preorbital)

[1]After Phillips (1957) and Chen (1971).
[2]After Matsubara (1943) and Weitzman (1962).

follows Weitzman (1962) as recommended by Poss.[6]

SEBASTES CRAMERI (JORDAN)
(Figures 2, 3, 4)

Literature.—Pigment patterns of preextrusion larvae of *S. crameri* were described by Westrheim et al.,[7] including one figure, and Westrheim (1975). Preextrusion larvae (mean total length = 5.7 mm) have a row of 10 to 23 melanophores (45% of 60 larvae had <16 melanophores) along the ventral body midline which stops short of the anus by four myomeres. Melanophore(s) are also usually present on the ventral finfold in the hypural region. The gut is pigmented. No pigment occurs on the head, nape, or dorsal body midline, however, Westrheim (1975) reported that *S. crameri* larvae, along with several other species, reared for several days develop pigment spots on the head, nape, and/or lower jaw.

Identification (Table 3, Appendix Tables 2-6).—Eighty-one specimens of *S. crameri*, ranging from 8.0 to 130.5 mm, were identified. Juveniles were identified using the following combination of characters recorded from specimens in our collections:

Gill rakers = 30-34
Lateral line pores = 43-50
Pectoral fin rays = 18-20, usually 19
Anal fin soft rays = 7
Dorsal fin soft rays = 13-15
Supraocular spine = present
Interorbital space = flat to convex.

No other species on our list of potential species agrees with all these characters. In addition, the characteristic pigment banding of adults was obvious on larger juveniles. Larvae and juveniles were relatively abundant in our collections and adults are known to be abundant in terms of biomass in trawl catches off the Oregon coast (Demory et al. 1976; Niska 1976). The developmental series was linked together primarily on the basis of pigmentation and also body shape and time of occurrence. Identification of most of the smaller specimens was further substantiated by meristics, particularly the constancy in number of anal and pectoral fin rays (Table 3).

[6]S. G. Poss, Ph.D. Candidate, Department of Zoology, University of Michigan, Ann Arbor, MI 48109, pers. commun. July 1977.

[7]Westrheim, S. J., W. R. Harling, and D. Davenport. 1968. Preliminary report on the maturity, spawning season and larval identification of rockfishes (*Sebastodes*) collected off British Columbia in 1967. Fish. Res. Board Can., Manuscr. Rep. 951, 23 p.

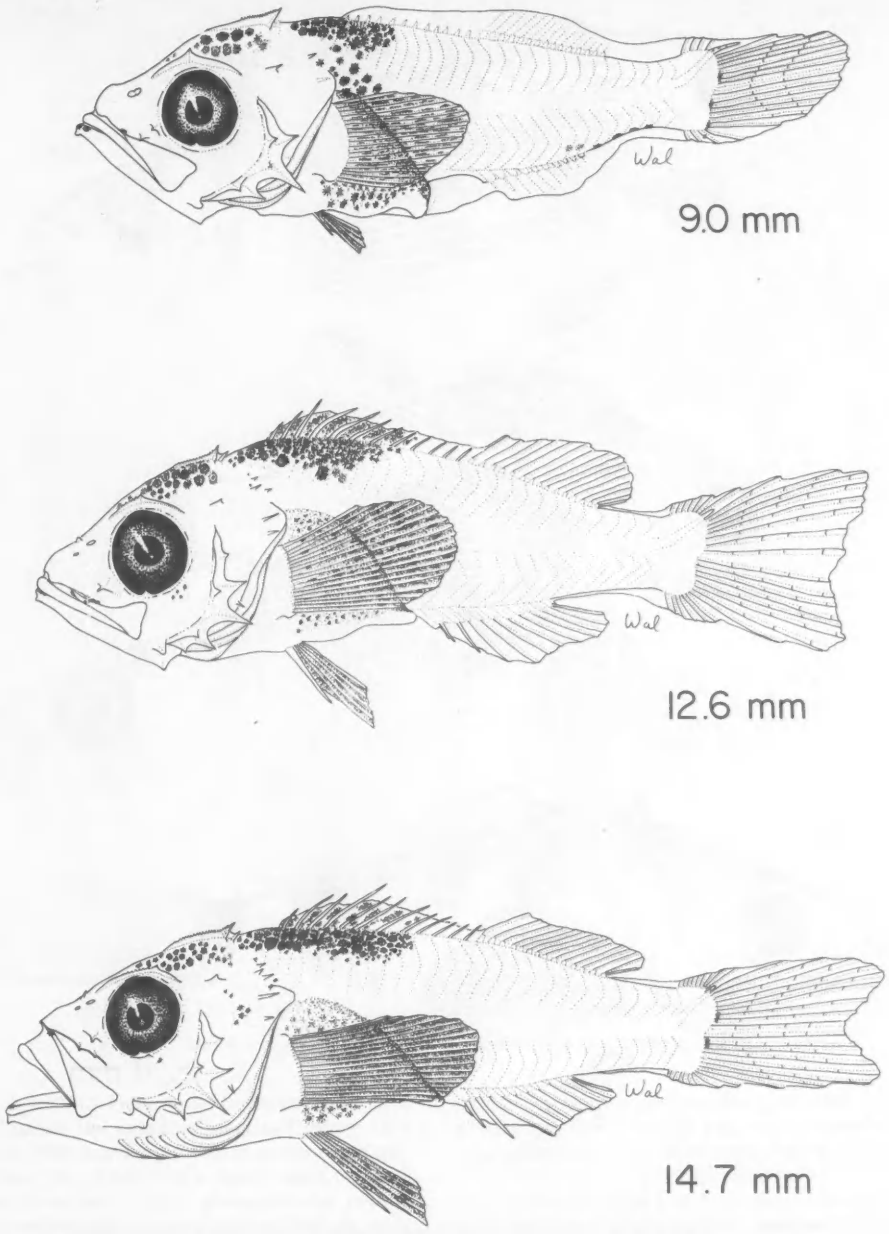

FIGURE 2.—Planktonic larvae (9.0, 12.6, 14.7 mm) of *Sebastes crameri*.

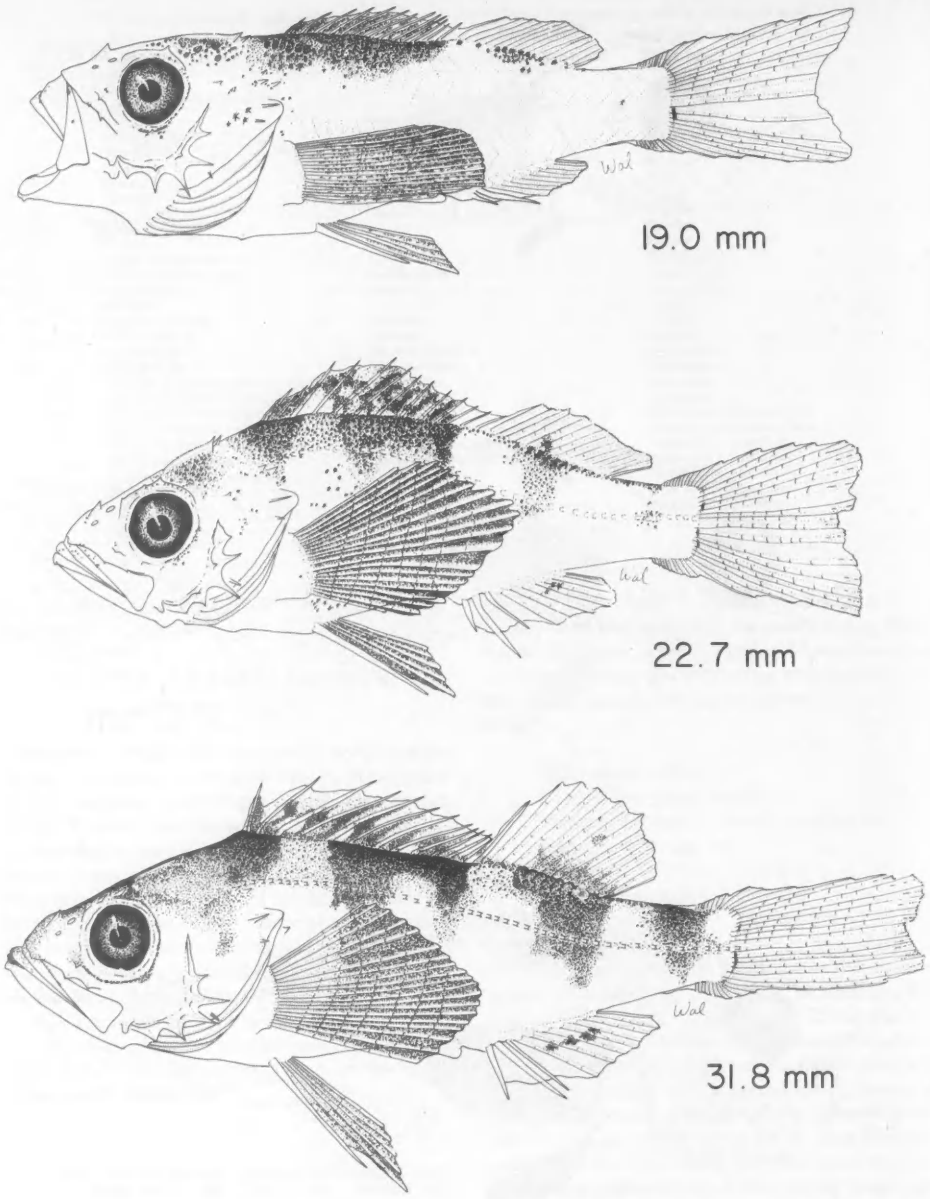

FIGURE 3.—Transforming specimen (19.0 mm) and pelagic juveniles (22.7, 31.8 mm) of *Sebastes crameri*.

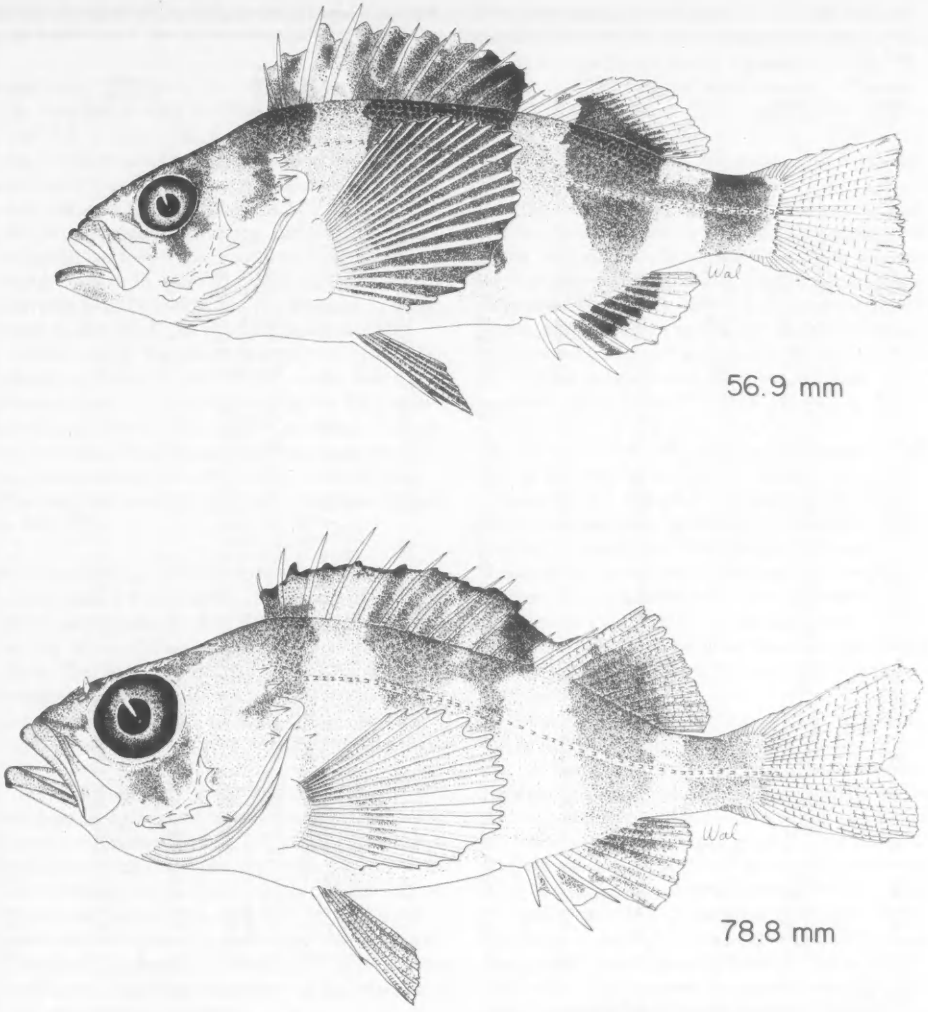

FIGURE 4.—Pelagic juvenile (56.9 mm) and benthic juvenile (78.8 mm) of *Sebastes crameri*.

Distinguishing Features.—Characters useful to distinguish the smallest identified larvae (8.0 mm) are the heavily pigmented pectoral and pelvic fins, the presence of a heavy nape pigment patch from which some melanophores extend down and over the gut externally on the body wall, the absence of dorsal midline pigment other than at the nape, the presence of ventral midline pigment as ≈11 distinct melanophores of which the anterior ones are embedded and only the posteriormost ones remain on the ventral body surface, and pigment at the tip of the lower jaw. The presence of pigment on the first dorsal fin in larvae as small as 11 mm is also a useful character. Meristics, presence of a supraocular spine, flat to convex shape of the interorbital space, heavily pigmented

TABLE 3.—Meristics from larvae and juveniles of *Sebastes crameri* off Oregon, based on unstained specimens. Specimens above dashed line are undergoing notochord flexion. All specimens had 8 superior and 7 inferior principal caudal fin rays and 7 branchiostegal rays on each side.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Pelvic fin spines and rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows
			Left	Right	Left	Right	Left	Right	Left	Right	
8.0	(1)	(1)	—	19	(2)	(2)	—	—	—	—	—
8.0	(1)	(1)	19	19	(2)	(2)	—	—	—	—	—
9.0	III+I,13-14	I,7	19	19	I,(1)	I,(1)	—	—	—	—	—
9.0	I,14	I,7	19	19	I,(1)	I,(1)	—	—	—	—	—
9.3	I,14	I,7	19	19	I,(1)	I,(1)	—	—	—	—	—
10.6	VI+I,13	I,7	19	19	I,5	I,5	—	—	—	—	—
10.6	VIII+I,14	II,7	19	19	I,5	I,5	—	—	—	—	—
10.7	IX+I,13	II,7	—	19	I,5	I,5	—	—	—	—	—
12.2	X+I,14	III,7	19	19	I,5	I,5	—	19+ 8=27	—	—	—
12.6	XI+I,13	III,7	19	19	I,5	I,5	—	≈19+ 8=27	—	—	—
12.8	XI+I,14	III,7	19	19	I,5	I,5	—	—	—	—	—
13.6	XIII,13	III,7	19	19	I,5	I,5	—	≈18+ 8=26	—	—	—
13.8	XIII,14	III,7	19	20	I,5	I,5	—	≈20+ 8=28	—	—	—
14.4	XIII,14	III,7	19	19	I,5	I,5	—	≈20+ 8=28	—	—	—
14.7	XIII,14	III,7	20	19	I,5	I,5	—	21+ 9=30	—	—	—
15.4	XIII,14	III,7	18	18	I,5	I,5	—	—	—	—	—
4 16.0	XIII,14	III,7	19	19	I,5	I,5	—	21+ 8=29	—	—	—
4 16.3	XIII,14	III,7	19	19	I,5	I,5	—	22+ 8=30	—	—	—
4 17.3	XIII,13	III,7	19	19	I,5	I,5	—	21+ 9=30	—	—	—
4 17.4	XIII,13	III,7	19	19	I,5	I,5	—	22+ 9=31	—	—	—
4 18.2	XIII,14	III,7	19	19	I,5	I,5	—	20+ 9=29	—	—	—
4 18.4	XIII,13	III,7	20	19	I,5	I,5	—	22+ 9=31	—	—	—
4 18.6	XIII,14	III,7	20	20	I,5	I,5	—	22+ 8=30	—	—	—
4 19.0	XIII,14	III,7	19	20	I,5	I,5	—	22+10=32	—	—	—
4 20.0	XIII,14	III,7	19	19	I,5	I,5	21+ 9=30	22+ 9=31	—	—	—
4 20.3	XIII,14	III,7	19	19	I,5	I,5	22+ 9=31	22+ 9=31	—	—	—
4 21.0	XIII,14	III,7	19	19	I,5	I,5	22+ 9=31	21+ 9=30	—	—	—
5 22.7	XIII,13	III,7	20	20	I,5	I,5	22+ 9=31	22+ 9=31	—	—	—
5 23.5	XIII,13	III,7	19	19	I,5	I,5	23+ 9=32	22+10=32	—	—	—
5 24.2	XIII,14	III,7	19	19	I,5	I,5	23+ 9=32	22+ 9=31	—	—	—
5 25.6	XIII,15	III,7	19	20	I,5	I,5	22+ 9=31	23+ 9=32	—	—	—
5 28.6	XIII,14	III,7	19	19	I,5	I,5	22+ 9=31	23+10=33	—	—	—
5 30.0	XIII,13	III,7	19	19	I,5	I,5	22+ 9=31	23+ 9=32	≈48	≈47	—
5 31.8	XIII,13	III,7	19	19	I,5	I,5	23+10=33	22+10=32	46	—	—
5 35.7	XIII,14	III,7	19	19	I,5	I,5	23+ 9=32	23+ 9=32	45	≈43	—
5 38.2	XIII,14	III,7	19	19	I,5	I,5	23+10=33	23+ 9=32	—	—	—
5 56.9	XIII,14	III,7	19	19	I,5	I,5	22+ 9=31	22+ 9=31	45	46	—
5 46.8	XIII,13	III,7	19	19	I,5	I,5	24+ 9=33	23+ 9=32	≈48	—	—
5 49.2	XIII,14	III,7	19	19	I,5	I,5	23+10=33	24+10=34	≈43	≈46	—
6 58.9	XIII,14	III,7	19	19	I,5	I,5	22+ 9=31	22+ 9=31	45	45	—
6 63.0	XIII,14	III,7	19	19	I,5	I,5	23+ 9=32	23+ 9=32	45	46	—
6 63.2	XIII,13	III,7	19	19	I,5	I,5	22+ 9=31	23+ 9=32	50	46	—
6 65.0	XIII,14	III,7	19	20	I,5	I,5	24+ 9=33	24+ 9=33	49	50	—
6 67.6	XIII,14	III,7	19	19	I,5	I,5	22+10=32	23+10=33	47	48	—
6 78.8	XIII,14	III,7	19	19	I,5	I,5	22+ 9=31	22+ 9=31	48	44	—
6 86.1	XIII,13	III,7	19	18	I,5	I,5	23+ 9=32	23+ 9=32	46	46	—
6 91.8	XIII,14	III,7	19	19	I,5	I,5	22+10=32	23+10=33	47	49	≈53
6 94.4	XIII,14	III,7	19	19	I,5	I,5	22+ 8=30	22+ 9=31	49	47	≈59
6 94.7	XIII,14	III,7	19	20	I,5	I,5	23+10=33	23+ 9=32	45	45	—
6 96.2	XIII,13	III,7	19	18	I,5	I,5	22+ 9=31	22+ 9=31	47	45	≈55
6 105.6	XIII,13	III,7	19	19	I,5	I,5	22+ 9=31	22+ 9=31	47	47	≈51
6 125.7	XIII,14	III,7	19	19	I,5	I,5	23+ 9=32	23+10=33	45	44	≈59
6 130.5	XIII,13	III,7	20	20	I,5	I,5	23+10=33	23+ 9=32	46	47	≈60

[1] Forming.
[2] Not formed.
[3] Posteriormost dorsal or anal spine appears as a soft ray.
[4] Transforming.
[5] Pelagic juvenile.
[6] Benthic juvenile.

pectoral and pelvic fins, and pigment banding pattern on the body serve to distinguish juveniles.

General Development.—The smallest specimens (8.0-9.0 mm) of *S. crameri* in the series are undergoing the final stages of notochord flexion, which is completed by the time larvae are 10 mm. Transformation from postflexion larvae to pelagic juveniles is rather gradual beginning when larvae are about 16 mm. It is characterized by addition of pigment beneath the second dorsal fin along with initiation of structural change of the "prespines" in the dorsal and anal fins. Transformation is complete in 22 mm specimens and the juvenile pigment pattern is obvious. Transition from pelagic to benthic habitat probably occurs when fish are 40 to 60 mm. The largest pelagic juvenile, captured in a neuston net, was 56.9 mm and the

smallest juvenile taken in a bottom trawl was 46.8 mm.

Morphology (Tables 4, 5).—Measurements of various body parts were made on 53 selected specimens of *S. crameri*, ranging from 8.0 to 130.5 mm long, to examine developmental morphology. Relative body depth at the pectoral fin base and at the anus increases somewhat, 32 to 34% SL and 24 to 28% SL, respectively, during development from flexion larvae to benthic juveniles. A more marked change occurs in snout to anus distance which increases from 54 to 65% SL. The distance from the snout to the pelvic fin base increases slightly.

Head length decreases somewhat during development from 39 to 36% SL, while major decreases occur in eye diameter (40-33% HL), upper jaw length (56-41% HL), and interorbital distance (36-23% HL). Snout length first increases slightly and then decreases with respect to head length. The length of the angle gill raker increases from 9 to 16% HL.

Fin Development (Tables 3, 4, 5).—Pectoral fins are formed in 8 mm larvae of *S. crameri* and the adult complement of 18 to 20 (usually 19) fin rays (or ray elements) are countable in 9 mm specimens. The fins become more elongate with development, increasing from 17% SL in flexion larvae to a maximum of 32% SL in pelagic juveniles. Depth of the pectoral fin base decreases from 13 to 10% SL.

Pelvic fin buds are present on 8 mm larvae and the forming spines and rays (I, 5) can be counted in 9 mm larvae although they are not fully developed until the larvae reach about 10 mm. Length of the pelvic fins increased from 7 to 21% SL during the larval and juvenile periods. Length of the pelvic spine, which is less than the longest ray, increases from 5% SL in flexion larvae to 19% during transformation, and then decreases to an average of 13% in benthic juveniles.

In 8.0 mm larvae the adult complement of 8 + 7 principal caudal rays can be counted although notochord flexion does not appear to be complete until larvae are >9.3 mm. Counts of superior and inferior secondary caudal rays made on one stained juvenile, 38.2 mm, were 12 and 13, respectively.

Bases of some dorsal and anal fin rays and spines are visible on 8 mm larvae. Development of the second dorsal and anal soft rays occurs simultaneously with the central rays forming first and the posteriormost rays last. Developing soft ray elements are visible and adult complements can be counted on 9 mm larvae although rays do not appear fully formed until larvae are >10 mm. Dorsal spines begin to form slightly after initiation of soft ray formation at ≈9 mm. The third, fourth, and fifth dorsal spines develop first. The 12th spine is not formed until larvae are >13 mm long. The second anal spine is formed at 10.6 mm and the first is formed by 12 mm. The transition of dorsal and anal fin "prespines" to spines is complete at around 22 mm. The longest dorsal spine increases from 22 to 45% HL during the pelvic phase, and decreases to 37% in benthic juveniles. The longest dorsal ray increases from 26 to 41-43% HL during development. The longest anal spine increases from 16 to 37 or 38% HL.

Spination (Tables 4, 6).—Spines visible on the left side of the head of an 8.0 mm larva of *S. crameri* consist of the parietal; the second, third, and fourth preopercular spines of the posterior series; the first, second, and third preopercular spines of the anterior series; the postocular; and the pterotic. Another more developed 8.0 mm specimen has a developing nuchal spine bump; the inferior posttemporal; the first spine of the inferior infraorbital series, and the first spine on the superior infraorbital series.

The parietal spine is relatively short, averaging 6.5 to 6.6% HL in larvae and decreasing to 3.0% HL in pelagic juveniles. The nuchal spine increases in length from 1% HL in flexion larvae to 4% in postflexion and transforming specimens then decreases to 3% in pelagic juveniles. Parietal and nuchal spines begin to fuse near their bases at 10.7 mm, gradually fusing towards the tips until in specimens >38 mm the parietal tip is no longer visible. In benthic juveniles the nuchal and parietal spines are fused and their relative lengths are ≈2% HL; however, increased pigment and musculature allowed measurement only from tip to body junction. The parietal spine and ridge are not serrated in larvae <9 mm. Serrations first appear at the center of the parietal ridge at 9 mm and persist until ≈39 mm.

The posterior series of preopercular spines are among the most prominent in the larvae. The first through fifth spines of the series are present in larvae >10 mm. The third spine of the series is the largest, averaging 17 or 18% HL in larvae and then decreasing to 7% HL in benthic juveniles. Spines in the posterior preopercular series never

TABLE 4.—Body proportions of larvae and juveniles of *Sebastes crameri*, *S. pinniger*, and *S. helvomaculatus*. Values given are percent standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. (Number of specimens measured may be derived from Tables 5, 8, and 11.)

Item	*Sebastes crameri*	*Sebastes pinniger*	*Sebastes helvomaculatus*
Body depth at pectoral fin base/SL:			
Flexion	31.8±2.05(29.0-33.8)	40.3±0.92(39.7-41.0)	33.3±1.44(32.5-35.0)
Postflexion	31.7±1.26(30.3-34.9)	38.1±2.51(33.7-42.0)	33.4±0.46(33.0-33.9)
Transforming	32.4±1.74(29.5-35.6)	35.9±1.36(33.3-38.3)	32.6±1.79(30.6-35.8)
Pelagic Juvenile	32.7±1.89(30.3-37.4)	33.0±1.88(29.8-37.0)	31.2±1.58(28.4-32.9)
Benthic Juvenile	34.4±1.96(30.1-36.5)	34.9±2.15(32.7-37.0)	33.4±1.63(32.3-34.6)
Body depth at anus/SL:			
Flexion	23.6±0.67(22.6-24.4)	27.6±0.92(26.9-28.2)	20.7±0.61(20.0-21.2)
Postflexion	24.9±1.19(22.6-26.5)	28.5±1.92(24.7-30.6)	24.5±2.56(21.6-26.3)
Transforming	26.7±1.34(24.7-29.4)	27.6±1.63(24.8-30.9)	24.7±1.22(23.1-26.9)
Pelagic Juvenile	26.8±1.15(25.2-29.2)	26.0±1.11(23.9-28.0)	23.2±1.24(21.2-25.0)
Benthic Juvenile	27.7±1.56(25.1-30.7)	29.8±3.68(27.3-34.0)	25.4±2.33(23.7-27.0)
Snout to anus length/SL:			
Flexion	54.0±1.28(52.5-55.9)	58.8±1.63(57.7-60.0)	56.1±1.28(55.0-57.5)
Postflexion	60.5±3.25(55.1-65.1)	59.6±3.42(51.7-62.6)	59.1±0.50(58.6-59.6)
Transforming	61.0±3.26(54.3-65.0)	60.6±1.84(58.1-63.1)	61.7±1.86(59.2-64.5)
Pelagic Juvenile	61.6±2.63(57.9-64.3)	61.4±3.50(56.0-67.4)	62.8±2.46(59.8-66.0)
Benthic Juvenile	65.0±1.81(61.5-68.7)	64.2±3.27(60.6-67.0)	63.8±1.06(63.0-64.5)
Snout to pelvic fin origin/SL:			
Flexion	37.6±1.56(35.0-38.9)	41.1±3.61(38.5-43.6)	40.5±1.27(39.0-41.2)
Postflexion	40.8±2.02(38.1-44.3)	40.7±3.03(34.7-44.9)	40.9±0.45(40.4-41.3)
Transforming	39.8±3.49(34.1-46.5)	41.9±2.74(38.7-46.2)	42.8±3.13(38.0-47.3)
Pelagic Juvenile	38.9±3.23(34.0-44.5)	39.9±3.83(32.9-45.5)	42.8±3.16(39.3-48.2)
Benthic Juvenile	40.5±1.86(37.3-43.1)	42.7±2.86(41.0-46.0)	40.0±0.92(39.4-40.7)
Head length/SL:			
Flexion	39.0±1.55(37.5-41.1)	43.0±0.92(42.3-43.6)	41.4±1.27(40.0-42.5)
Postflexion	38.9±1.90(36.8-43.4)	42.4±2.58(38.2-47.7)	42.0±2.03(40.4-44.3)
Transforming	36.6±2.43(32.8-38.7)	40.5±1.39(38.0-42.6)	40.8±1.92(36.4-43.0)
Pelagic Juvenile	35.8±1.82(32.3-38.3)	37.5±2.52(33.3-42.1)	40.1±1.48(37.5-41.9)
Benthic Juvenile	36.4±2.75(31.8-39.9)	36.6±0.51(36.0-37.0)	37.6±0.57(37.2-38.0)
Eye diameter/HL:			
Flexion	40.2±1.82(37.8-42.9)	37.3±1.27(36.4-38.2)	38.8±1.63(29.4-31.2)
Postflexion	38.2±1.87(33.9-40.0)	39.3±1.89(37.5-41.3)	36.3±0.36(35.9-36.6)
Transforming	36.9±2.47(33.3-42.1)	37.5±1.35(34.2-38.7)	35.5±2.38(32.0-38.8)
Pelagic Juvenile	30.4±2.60(26.6-35.0)	34.2±2.77(30.8-42.3)	33.6±1.76/30.8-36.9)
Benthic Juvenile	31.6±2.05(28.9-35.6)	26.8±3.22(24.0-30.3)	31.6±5.30(27.8-35.3)
Upper jaw length/HL:			
Flexion	46.5±4.35(40.5-50.0)	47.8±0.99(47.1-48.5)	45.0±3.29(41.2-46.9)
Postflexion	43.6±2.45(40.0-46.3)	46.1±3.73(41.2-52.4)	44.0±3.00(41.0-47.0)
Transforming	43.8±5.55(34.2-50.9)	42.1±3.64(35.6-47.0)	45.7±4.23(39.7-53.1)
Pelagic Juvenile	41.3±4.06(33.9-47.5)	41.3±3.14(34.6-47.4)	45.1±2.63(40.2-47.6)
Benthic Juvenile	41.2±2.44(37.8-45.6)	44.9±2.15(42.7-47.0)	52.1±0.78(51.5-52.6)
Snout length/HL:			
Flexion	29.1±1.38(27.0-30.7)	26.9±0.28(26.7-27.1)	32.3±2.20(30.0-34.4)
Postflexion	30.0±1.65(26.1-31.7)	28.7±3.45(23.8-34.8)	33.0±1.18(31.7-34.1)
Transforming	31.2±2.69(27.0-35.6)	30.2±3.31(25.8-36.5)	32.4±3.72(25.0-37.9)
Pelagic Juvenile	28.2±2.97(24.6-32.1)	27.3±3.68(21.7-32.5)	31.7±2.49(26.7-34.1)
Benthic Juvenile	26.3±2.43(22.4-31.2)	28.8±0.72(28.0-29.4)	26.7±0.42(26.4-27.0)
Interorbital distance/HL:			
Flexion	35.6±1.95(32.4-37.1)	37.3±1.27(36.4-38.2)	30.6±1.04(29.4-31.2)
Postflexion	33.0±1.94(29.3-36.0)	34.2±2.26(30.4-38.2)	31.4±0.55(30.8-31.8)
Transforming	31.2±3.39(25.9-36.8)	30.0±1.82(26.3-32.3)	27.0±2.89(23.3-30.6)
Pelagic Juvenile	25.9±2.48(23.0-30.0)	24.4±3.31(19.5-30.8)	21.5±3.83(13.3-25.6)
Benthic Juvenile	21.6±2.18(18.0-26.8)	19.8±1.37(18.3-21.0)	14.6±2.47(12.9-16.4)
Angle gill raker length/HL:			
Flexion	8.6±0.00(8.6)	—	—
Postflexion	11.4±1.77(8.6-14.4)	10.6±1.42(8.3-12.3)	13.4±0.95(12.3-14.1)
Transforming	13.1±1.13(11.1-15.1)	13.0±0.72(11.5-14.5)	15.1±1.46(12.9-18.0)
Pelagic Juvenile	13.9±0.82(13.3-15.1)	14.1±1.21(11.7-16.5)	14.2±1.90(12.7-15.7)
Benthic Juvenile	15.8±1.06(13.7-17.4)	14.9±1.10(13.8-16.0)	10.6±0.50(10.3-11.0)
Longest dorsal spine length[1]/HL:			
Flexion	—	—	—
Postflexion	21.6±2.26(19.4-24.1)	20.1±6.05(13.0-28.8)	19.0±0.64(18.6-19.5)
Transforming	34.3±7.13(26.2-45.1)	32.4±5.49(23.6-40.6)	29.2±6.08(22.4-37.5)
Pelagic Juvenile	44.7±1.55(42.0-46.2)	38.0±3.79(33.1-46.2)	30.9±2.93(28.0-35.7)
Benthic Juvenile	36.9±4.32(31.7-44.3)	35.6±4.74(32.0-41.0)	37.0±4.88(33.6-40.5)
Longest dorsal ray length[2]/HL:			
Flexion	—	—	22.8±7.39(15.9-30.6)
Postflexion	26.2±6.96(14.6-33.3)	31.5±4.26(23.8-38.0)	26.4±5.14(20.5-29.5)
Transforming	41.4±2.32(39.3-43.9)	38.5±3.60(30.8-42.9)	36.1±3.06(32.5-41.7)
Pelagic Juvenile	42.0±2.97(38.1-46.7)	41.6±3.46(35.4-48.7)	35.1±2.53(32.0-38.1)
Benthic Juvenile	43.1±4.74(37.6-48.1)	42.6±3.83(40.0-47.0)	42.8±3.89(40.0-45.5)
Longest anal spine length[3]/HL:			
Flexion	—	—	—
Postflexion	15.6±3.16(9.6-18.5)	18.7±2.52(14.6-21.3)	16.0±1.91(14.6-17.3)
Transforming	28.1±3.46(23.0-32.0)	28.5±5.65(20.0-38.6)	27.3±4.46(22.4-36.1)

TABLE 4.—Continued.

Item	*Sebastes crameri*	*Sebastes pinniger*	*Sebastes helvomaculatus*
Pelagic Juvenile	37.8±4.36(31.2-43.5)	37.4±4.07(30.8-44.0)	32.4±5.70(26.8-38.1)
Benthic Juvenile	36.5±4.34(30.6-44.3)	34.5±2.50(32.0-37.0)	48.8±4.67(45.5-52.1)
Pectoral fin length/SL:			
Flexion	17.1±1.52(15.0-18.9)	25.0±2.69(23.1-26.9)	23.6±2.11(21.2-25.0)
Postflexion	21.1±2.26(17.0-23.5)	24.7±2.64(20.2-28.5)	24.4±0.57(23.9-25.0)
Transforming	27.1±1.54(24.7-29.5)	27.0±2.42(22.7-31.5)	26.0±1.45(24.3-28.3)
Pelagic Juvenile	32.1±1.73(30.2-35.3)	26.2±1.36(24.0-28.5)	26.6±0.28(26.1-26.9)
Benthic Juvenile	29.5±3.61(25.0-38.9)	24.3±1.21(22.9-25.0)	27.0±0.85(26.4-27.6)
Pectoral fin base depth/SL:			
Flexion	12.6±1.27(10.8-13.8)	14.8±0.92(14.1-15.4)	12.5±0.00(12.5)
Postflexion	11.1±0.39(10.4-11.8)	12.6±0.83(11.4-13.6)	11.5±0.84(11.0-12.5)
Transforming	10.4±0.61(9.5-11.7)	10.7±0.59(9.7-11.5)	9.9±0.64(9.0-10.8)
Pelagic Juvenile	9.6±0.51(8.5-10.2)	9.1±0.64(8.2-10.1)	9.0±0.33(8.2-9.1)
Benthic Juvenile	10.2±0.53(8.8-10.9)	8.9±0.23(8.6-9.0)	9.3±0.71(8,8-9.8)
Pelvic fin length/SL:			
Flexion	7.3±1.81(5.2-9.8)	13.8±2.19(12.3-15.4)	13.5±1.32(12.5-15.0)
Postflexion	15.3±1.46(12.3-16.9)	17.2±4.12(10.0-22.8)	15.5±0.70(14.8-16.2)
Transforming	20.6±1.01(18.3-22.1)	22.7±1.59(20.8-25.3)	19.3±1.62(16.7-21.6)
Pelagic Juvenile	20.9±0.60(20.1-21.9)	21.7±1.29(19.4-23.7)	19.2±1.36(17.3-21.4)
Benthic Juvenile	20.7±0.97(18.5-22.2)	21.3±2.08(19.0-23.0)	22.7±0.99(22.0-23.4)
Pelvic spine length/SL:			
Flexion	4.7±1.42(3.4-6.2)	5.1±0.00(5.1)	8.3±0.15(8.2-8.5)
Postflexion	11.4±2.20(6.8-14.6)	12.1±2.99(8.2-15.0)	12.3±2.26(10.2-14.7)
Transforming	18.8±1.65(14.5-20.1)	19.5±1.38(17.6-21.7)	17.6±1.02(15.8-19.1)
Pelagic Juvenile	19.0±1.35(16.2-20.7)	17.9±2.10(14.5-22.1)	16.4±1.99(13.5-18.9)
Benthic Juvenile	13.9±1.34(12.3-17.1)	12.5±0.50(12.0-13.0)	14.9±0.71(14.4-15.4)
Parietal spine length/HL:			
Flexion	6.5±1.01(5.4-7.4)	24.4±0.35(24.2-24.4)	27.4±4.19(22.9-31.2)
Postflexion	6.6±1.06(5.2-8.5)	19.5±7.17(8.8-23.5)	18.5±2.24(15.9-20.0)
Transforming	6.0±1.24(3.7-7.4)	10.2±3.07(3.9-12.9)	12.6±2.39(9.0-16.3)
Pelagic Juvenile	2.9±0.98(1.8-4.2)	7.1±2.66(5.4-10.2)	5.6±3.31(1.1-9.5)
Benthic Juvenile	—	—	3.1±0.00(3.1)
Nuchal spine length/HL:			
Flexion	1.1±0.00(1.1)	—	1.8±0.85(1.2-2.4)
Postflexion	4.1±0.73(3.4-5.8)	4.4±1.63(2.5-6.9)	4.3±1.51(2.6-5.0)
Transforming	4.4±0.88(3.1-6.0)	4.8±1.57(2.3-7.2)	4.6±0.78(3.0-4.9)
Pelagic Juvenile	3.2±1.03(2.0-5.0)	3.1±0.96(1.9-5.4)	3.5±1.13(1.7-5.2)
Benthic Juvenile	1.7±0.64(0.7-2.8)	1.4±0.64(1.0-2.1)	—
Preopercular spine length/HL:			
Flexion	17.6±3.84(12.0-20.5)	34.4±2.83(32.4-36.4)	27.4±4.19(22.9-31.2)
Postflexion	17.0±1.09(15.5-18.5)	31.8±4.86(25.0-39.0)	31.2±0.64(30.8-31.7)
Transforming	18.3±1.53(16.0-19.7)	23.6±2.09(21.2-29.1)	20.2±3.58(16.2-26.5)
Pelagic Juvenile	12.0±2.85(8.6-16.2)	12.8±3.96(9.1-22.2)	11.8±6.29(2.5-15.9)
Benthic Juvenile	7.2±2.72(3.1-11.4)	4.8±1.39(4.0-6.4)	1.6±1.34(0.6-2.5)

[1]Usually third or fourth in larvae, fifth or sixth in juveniles.
[2]Usually midfin.
[3]The second spine.

develop strong serrations. Spines in the anterior preopercular series are much shorter than those in the posterior series. The second or middle spine is present only in larvae prior to completion of notochord flexion, <10 mm. Its appearance as a spine changes to a small bump which then fuses with the ridges connecting it to the third preopercular spine of the posterior series. The first and third anterior spines are present on larvae through pelagic juveniles of ≈23 mm and then are no longer visible.

The superior and inferior opercular spines and the interopercular spine appear by the time the larvae reach 12 mm, although percursor bumps may be seen as early as 9 mm. These spines persist into the juvenile stage. The subopercular spine is present in juveniles >78 mm.

Around the eye, the ridge anterior to the postocular spine becomes serrated at 10.6 mm. These serrations disappear at the time of supraocular spine formation, >21 mm. The preocular spine begins to appear in transforming specimens >16 mm and is strongly formed by the time fish are 20 mm. Beneath the eye the second spine of the inferior infraorbital series forms in larvae >10 mm. The fourth spine of the superior infraorbital series develops under the posterior third of the eye on larvae >13.6 mm and it persists through the juvenile stage as do the two inferior infraorbital spines. The second and third superior and third inferior infraorbital spines never develop. Tiny serrations appear along a ridge between the first and fourth superior infraorbital spines in specimens 14.4 to 38.2 mm. The first spine of the superior infraorbital series disappears in specimens >50 mm. The nasal spine develops in larvae of ≈10 mm and persists in juveniles.

TABLE 5.—Measurements (millimeters) of larvae and juveniles of *Sebastes crameri* from waters off Oregon. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
8.0	9.4	4.2	3.0	0.88	1.5	1.2	1.1	2.7	1.9	1.2	1.1	[4]	0.52	2.8	0.20	[4]	0.56	—	[4]	[4]	[4]
8.0	9.7	4.3	3.0	0.92	1.5	1.2	1.1	2.7	1.9	1.4	1.1	[4]	0.52	3.0	—	—	0.36	—	[4]	[4]	[4]
9.0	11.2	4.9	3.7	1.0	1.5	1.4	1.2	2.8	2.2	1.6	1.1	0.56	0.76	3.4	0.20	0.04	0.76	—	[4]	[4]	[4]
9.0	10.7	4.8	3.5	1.0	1.7	1.5	1.3	2.8	2.1	1.7	1.1	0.40	0.88	3.5	0.26	[4]	0.68	—	[4]	[4]	[4]
9.3	11.4	5.2	3.7	1.1	1.6	1.5	1.3	2.7	2.1	1.5	1.0	0.32	0.48	3.6	—	—	—	0.32	[4]	[4]	[4]
10.6	12.8	6.3	4.1	1.3	1.9	1.6	1.4	3.3	2.4	1.8	1.2	0.72	1.3	4.2	0.28	—	—	0.36	[4]	0.60	[4]
10.6	13.0	6.9	4.6	1.4	2.1	1.7	1.5	3.7	2.8	1.9	1.2	1.1	—	4.7	—	—	—	0.50	[4]	0.88	0.44
10.7	13.4	—	—	—	—	—	—	3.4	2.6	—	—	1.2	1.5	—	0.28	—	—	—	0.60	1.2	—
12.2	15.0	7.3	4.6	1.2	2.0	1.8	1.5	3.7	3.0	2.5	1.4	1.5	1.8	4.8	—	0.20	0.80	0.50	0.92	1.4	0.76
12.6	15.8	7.2	4.8	1.4	2.0	1.9	1.6	3.9	3.0	2.8	1.4	1.6	2.0	4.8	0.32	0.28	0.80	0.50	1.1	1.5	0.80
12.8	15.8	7.5	5.0	1.6	2.0	2.0	1.7	4.2	3.3	2.8	1.4	1.3	2.1	5.4	—	0.20	0.84	0.50	—	1.1	0.60
13.6	16.0	7.5	5.0	1.5	2.0	2.0	1.8	4.3	3.4	3.2	1.5	—	2.3	5.2	0.36	0.20	—	0.60	—	—	0.92
13.8	16.0	8.3	5.2	1.6	2.2	2.0	1.8	4.4	3.5	3.0	1.5	1.6	2.0	5.6	0.30	0.20	—	0.64	—	—	—
14.4	17.3	9.3	5.4	1.6	2.5	2.0	1.8	4.5	3.7	3.1	1.7	2.1	2.2	6.0	0.46	0.20	1.0	0.78	—	1.8	1.0
14.7	17.6	9.2	5.8	1.7	2.6	2.2	1.7	4.5	3.9	—	1.6	1.9	2.4	6.2	0.36	0.20	—	0.82	1.4	1.9	1.0
15.4	18.1	9.7	6.2	1.9	2.8	2.1	1.9	4.9	3.7	3.6	1.6	—	2.6	6.5	0.32	0.24	0.96	0.66	1.2	1.6	1.0
[5]16.0	20.0	9.5	6.1	2.0	—	2.3	2.1	5.2	4.3	4.1	1.7	—	3.4	6.2	0.44	—	—	0.72	1.6	2.4	1.4
[5]16.3	20.3	10.3	6.3	1.7	3.0	2.3	2.0	5.8	4.8	—	1.9	3.1	3.6	6.3	0.42	0.28	1.2	0.86	2.2	—	—
[5]17.3	20.5	10.0	6.7	2.2	3.0	2.4	2.0	5.8	4.7	5.1	1.8	2.8	3.4	7.1	0.46	0.28	—	0.88	2.0	—	1.7
[5]17.4	21.8	10.7	5.7	1.9	2.9	2.4	2.1	5.8	4.6	4.8	1.9	3.2	3.6	6.7	0.42	0.34	—	0.86	—	2.5	1.5
[5]18.2	21.6	10.7	6.2	1.7	2.9	2.4	2.2	6.0	5.1	—	2.0	3.2	3.8	6.2	0.40	0.30	1.2	0.84	2.2	—	—
[5]18.4	23.4	11.0	6.6	2.0	3.2	2.6	2.1	6.3	5.1	4.7	1.9	3.7	—	6.7	0.40	0.28	1.1	0.92	—	—	2.1
[5]18.6	22.7	10.1	6.4	2.0	2.8	2.4	1.8	5.8	4.8	4.6	1.9	2.7	3.4	7.1	—	0.36	1.2	0.88	—	2.2	2.0
[5]19.0	24.0	12.2	7.3	2.6	2.5	2.6	2.0	5.8	4.7	5.2	1.9	3.4	3.9	8.1	0.42	0.34	—	0.94	—	3.0	2.0
[5]20.0	24.8	13.0	8.1	2.7	3.4	2.7	2.1	5.9	5.1	5.5	2.0	3.9	4.2	9.3	0.34	0.28	—	0.90	—	—	2.0
[5]20.3	24.5	13.0	7.1	2.1	3.2	2.5	2.2	6.4	5.2	5.5	2.0	3.7	4.2	7.9	0.38	0.22	1.4	0.90	3.2	—	2.2
[5]21.0	25.3	13.1	7.5	2.2	2.6	2.6	2.3	6.7	5.5	6.0	2.0	4.0	4.4	9.2	0.28	0.30	1.2	0.90	—	—	2.4
[5]22.7	28.3	13.3	8.0	2.3	3.3	2.8	2.3	7.5	6.0	6.9	2.3	4.2	4.8	8.3	—	0.34	—	1.1	3.7	—	2.5
[5]23.5	28.3	13.6	8.0	2.0	3.8	2.7	2.4	7.6	6.4	7.3	2.4	—	5.0	8.0	0.34	0.40	1.3	1.2	3.7	3.4	3.0
[5]24.2	28.6	15.5	8.8	2.6	4.1	2.7	2.4	8.1	6.6	7.3	2.4	5.0	5.2	9.9	0.36	—	—	1.1	—	—	3.5
[5]25.6	32.3	16.3	9.8	3.1	3.9	2.7	2.6	8.2	7.0	8.4	2.4	5.3	5.6	11.4	0.30	0.38	1.5	1.3	—	3.8	—
[5]28.6	34.7	17.1	9.8	3.1	3.7	3.0	2.7	8.9	7.2	8.9	2.7	5.5	5.8	12.2	0.26	0.20	1.2	1.3	—	4.3	3.6
[5]30.0	35.2	17.6	11.2	2.8	3.8	3.4	2.7	9.1	7.6	9.3	2.8	5.8	6.2	11.7	0.20	0.28	1.1	1.5	4.7	—	—
[5]31.8	39.8	19.4	11.8	2.9	5.2	3.5	2.8	10.2	8.3	10.7	2.7	6.0	6.4	11.2	0.26	0.46	1.6	1.6	5.3	4.5	4.0
[5]35.7	45.1	22.9	13.1	3.4	5.4	3.7	3.2	11.7	9.6	12.6	3.5	6.8	7.4	13.9	0.26	0.34	1.4	1.9	6.0	5.6	5.5
[5]38.2	46.1	24.3	13.9	3.8	5.8	3.7	3.2	14.3	10.3	13.0	3.8	7.0	—	14.9	Joined	0.34	1.2	2.1	6.2	5.7	—
[6]56.9	68.7	36.6	18.4	5.9	7.2	5.7	4.3	18.7	16.6	17.8	5.7	9.2	11.6	21.6	Joined	0.48	1.7	2.6	8.0	8.6	8.0
[7]46.8	60.9	31.2	14.9	3.4	6.8	4.6	4.0	14.1	12.0	18.2	4.1	8.0	10.3	17.9	Joined	0.40	1.7	2.6	6.6	7.9	6.6
[7]49.2	60.7	32.0	16.3	4.7	7.0	5.8	4.0	15.0	12.8	16.0	4.8	7.1	10.5	19.2	Joined	0.34	1.7	2.6	6.5	7.6	—
[7]58.9	73.0	39.4	21.9	5.8	8.3	6.6	4.8	19.5	16.6	18.1	6.0	8.4	10.9	25.0	Joined	0.44	2.1	3.0	7.9	9.2	7.4
[7]63.0	76.2	41.8	20.8	6.5	9.3	7.2	4.6	20.5	15.8	19.5	5.9	9.0	12.5	26.4	Joined	0.56	1.7	3.5	8.0	10.0	8.0
[7]63.2	77.6	40.0	21.3	6.0	9.4	7.4	5.1	22.7	18.4	20.0	6.6	9.6	13.3	24.9	Joined	0.60	2.3	3.2	9.3	10.2	8.4
[7]65.0	80.6	40.0	22.6	6.6	8.9	6.6	4.9	22.9	18.4	21.4	6.7	—	14.4	27.4	Joined	0.38	2.1	3.8	8.5	10.7	9.5
[7]67.6	82.8	42.8	22.4	6.2	9.4	7.4	4.9	23.0	19.0	21.6	6.8	10.2	14.1	26.6	Joined	0.38	2.2	3.6	9.8	10.2	9.8
[7]78.8	96.6	51.5	30.3	6.8	13.0	9.8	5.9	27.6	20.7	21.8	7.7	9.8	15.8	32.3	Joined	0.40	2.1	4.8	9.6	12.5	9.8
[7]86.1	105.3	55.0	33.9	8.9	14.2	9.8	7.7	31.4	25.9	22.9	9.3	12.6	18.2	35.2	Joined	0.46	1.7	5.3	12.0	15.8	12.0
[7]91.8	112.3	63.1	36.6	9.3	14.2	11.2	6.6	30.9	25.0	23.8	9.3	11.5	18.4	36.8	Joined	0.60	1.8	5.9	11.7	14.1	11.7
[7]94.4	113.9	60.8	33.9	9.3	12.8	11.2	7.1	33.0	25.0	24.5	9.7	12.3	18.7	35.2	Joined	0.40	1.8	5.7	11.8	12.8	11.7
[7]94.7	114.7	61.5	36.2	8.6	15.2	11.2	7.5	33.6	26.4	23.7	9.8	11.8	20.0	40.2	Joined	0.44	1.9	5.1	12.5	14.4	12.6
[7]96.2	118.3	63.4	35.7	8.4	14.4	11.0	7.7	34.7	27.7	28.2	10.0	13.4	20.5	41.5	Joined	0.50	2.0	5.7	13.8	14.4	13.6
[7]105.6	128.2	67.0	41.2	10.7	16.3	12.8	8.5	38.0	32.4	28.8	10.7	13.6	20.8	45.2	Joined	0.44	2.0	6.8	13.1	15.7	12.6
[7]125.7	154.5	80.0	48.5	12.3	20.0	15.2	9.1	44.9	35.2	33.3	13.6	15.5	25.6	47.6	Joined	0.50	2.0	7.2	17.3	19.0	16.0
[7]130.5	160.9	86.6	51.0	13.3	19.7	14.9	10.4	46.6	35.6	37.3	14.2	18.4	28.0	52.2	Joined	0.36	1.6	7.4	16.3	19.2	17.6

[1]Usually third or fourth in larvae, fifth or sixth in juveniles.
[2]Usually midfin.
[3]The second spine.
[4]Not formed.
[5]Transforming.
[6]Pelagic juvenile.
[7]Benthic juvenile.

The tympanic spine, sometimes bifid, appears on specimens >25 mm. This spine forms at the anterior edge of a foramen of the cephalic lateral line system. The pterotic spine is present in flexion larvae and disappears in juveniles >50 mm. The supracleithral spine develops in larvae of ≈11 mm and the superior posttemporal spine can be seen on specimens >18 mm. These latter three spines persist in juveniles, however, the inferior posttemporal becomes reduced in larger juveniles. A cleithral spine develops dorsal to the pectoral fin base immediately posterior to the opercular margin on juveniles >30 mm.

Scale Formation.—Lateral line pores are visible on transforming specimens >18.2 mm. Developing scales are first visible on unstained specimens ≈20 mm on the posterodorsal region of the head and anterodorsal region of the trunk above the gut cavity. Scale development proceeds posteriorly with the body being covered by 29 mm.

Pigmentation.—Melanistic pigment on 8.0 mm specimens of *S. crameri* (similar to the 9 mm specimen illustrated) is present on the head over the brain. Melanophores line the inside tip of the lower jaw and may also be present along the anteroventral margin of the maxillary. In the abdominal region internal melanophores are densely concentrated on the dorsal surface of the gut and more sparsely distributed laterally and ventrally. Additional external melanophores are present on the body wall over the gut cavity. A heavy concentration of external melanophores and some in-

TABLE 6.—Development of spines in the head region of *Sebastes crameri* larvae and juveniles. Specimens above dashed line are undergoing notochord flexion. + denotes spine present and − denotes spine absent.

Standard length (mm)	Preopercular (anterior series)					Preopercular (posterior series)					Opercular		Interopercular	Subopercular	Preocular	Supraocular	Postocular
	Parietal	Nuchal	1st	2d	3d	1st	2d	3d	4th	5th	Superior	Inferior					
8.0	+	−	+	+	+	−	+	+	+	−	−	−	−	−	−	−	+
8.0	+	+	+	+	+	−	+	+	+	−	−	−	−	−	−	−	+
9.0	+	+	+	+	+	−	+	+	+	−	−	−	−	−	−	−	+
9.0	+	−	+	+	+	−	+	+	+	−	−	−	−	−	−	−	+
9.3	+	+	−	(1)	+	−	+	+	+	−	+	−	−	−	−	−	+
10.6	+	+	+	−	+	+	+	+	+	+	+	+	−	−	−	−	+
10.6	+	+	+	−	+	+	+	+	+	+	+	+	−	−	−	−	+
12.2	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
12.6	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
12.8	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
13.6	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
13.6	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
14.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
14.7	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
15.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]16.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]16.3	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]17.3	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]17.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]18.2	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]18.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]18.6	+	+	+	−	−	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]19.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]20.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	(1)	−	+
[2]20.3	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	−	+
[2]21.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	(1)	+
[3]22.7	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	(1)	+
[3]23.5	+	+	(1)	−	(1)	−	+	+	+	+	+	+	+	−	+	(1)	+
[3]24.2	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]25.6	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]28.6	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]30.0	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]31.8	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]35.7	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]38.2	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]56.9	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]46.8	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]49.2	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]58.9	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]63.0	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]63.2	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]65.0	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]67.6	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[4]78.8	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]86.1	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]91.8	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]94.4	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]94.7	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]96.2	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]105.6	+	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]125.7	+[5]	+[5]	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+
[4]130.5	+[5]	+[5]	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+

[1]Bump indicates beginning of spine formation.
[2]Transforming.
[3]Pelagic juvenile.
[4]Benthic juvenile.
[5]Parietal and nuchal spines fused.
[6]Spine is bifid.

TABLE 6.—Continued.

Standard length (mm)	Infraorbitals							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
8.0	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
8.0	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
9.0	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
9.0	–	–	–	+	–	–	–	–	–	–	+	–	+	–	–
9.3	–	–	–	+	–	–	–	–	–	–	+	–	+	–	–
10.6	+	–	–	+	–	–	–	(1)	–	–	+	–	+	–	–
10.6	+	+	–	+	–	–	–	(1)	–	–	+	–	+	+	–
12.2	+	+	–	+	–	–	–	+	–	–	+	–	+	+	–
12.6	+	+	–	+	–	–	–	+	–	–	+	–	+	+	–
12.8	+	+	–	+	–	–	–	+	–	–	+	–	+	+	–
13.6	+	+	–	+	–	–	–	+	–	–	+	–	+	+	–
13.8	+	+	–	+	–	–	(1)	+	–	–	+	–	+	+	–
14.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
14.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
15.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]16.0	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]16.3	+	+	–	+	–	–	–	+	–	–	+	–	+	+	–
[2]17.3	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]17.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]18.2	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]18.4	+	+	–	+	–	–	+	+	–	–	+	+	+	+	–
[2]18.6	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]19.0	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[2]20.0	+	+	–	+	–	–	+	+	–	–	+	+	+	+	–
[2]20.3	+	+	–	+	–	–	+	+	–	–	+	(1)	+	+	–
[2]21.0	+	+	–	+	–	–	+	+	–	–	+	+	+	+	–
[3]22.7	+	+	–	+	–	–	+	+	–	–	+	+	+	+	–
[3]23.5	+	+	–	+	–	–	+	+	–	–	+	+	+	+	–
[3]24.2	+	+	–	+	–	–	+	+	–	+	+	+	+	+	–
[3]25.6	+	+	–	+	–	–	+	+	–	+	+	+	+	+	–
[3]28.6	+	+	–	–	–	–	+	+	–	+	+	+	+	+	–
[3]30.0	+	+	–	+	–	–	+	+	–	+	+	+	+	+	–
[3]31.8	+	+	–	–	–	–	+	+	–	+[6]	+	+	+	+	+
[3]35.7	+	+	–	+	–	–	+	+	–	+[6]	+	+	+	+	+
[3]38.2	+	+	–	+	–	–	+	+	–	+	+	+	+	+	+
[3]56.9	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]46.8	+	+	–	+	–	–	–	+	–	+	+	+	+	+	+
[4]49.2	+	+	–	+	–	–	–	+	–	+[6]	+	+	+	+	+
[4]58.9	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]63.0	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]63.2	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]65.0	+	+	–	–	–	–	–	+	–	+[6]	–	+	+	+	+
[4]67.6	+	+	–	–	–	–	+	+	–	+[6]	–	+	+	+	+
[4]78.8	+	+	–	–	–	–	+	+	–	+[6]	–	+	+	+	+
[4]86.1	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]91.8	+	+	–	–	–	–	+	+	–	+[6]	–	+	+	+	+
[4]94.4	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]94.7	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]96.2	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]105.6	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]125.7	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+
[4]130.5	+	+	–	–	–	–	+	+	–	+	–	+	+	+	+

ternal pigment is present in the nape region although the dorsal midline is pigmentless. A few large stellate melanophores extend laterally from the nape to the gut cavity. A series of 10 or 11 distinct melanophores is visible along the ventral midline of the tail, the anterior five of which are embedded in musculature dorsal to the developing anal fin. A few small melanophores may be present on the notochord tip. The pectoral fins are distinctively and heavily pigmented. A dense concentration of melanophores occurs on the proximal surface of the fin base but the distal surface is unpigmented. Elongate melanophores line the inner and outer surfaces of the fin blades creating a striated appearance. The developing pelvic fins are also pigmented.

As larvae develop, pigment increases on the head over the brain. Melanophores persist along the tip of the lower jaw and the anteroventral margin of the maxillary. Several melanophores develop around the bases of the posttemporal and supracleithral spines in larvae >10.5 mm and on the dorsal part of the operculum anterior to the opercular spines in larvae >13.5 mm.

Pigmentation within the gut cavity remains intense through larval development and external melanophores remain scattered on the body wall over the gut. In larvae >10.5 mm, as dorsal fin

spines develop, melanophores are added to the nape patch along the dorsal midline and posteriorly along the dorsolateral body surface. The large stellate melanophores extending from the nape patch to the gut disappear by 12 mm. A few external melanophores appear along the anterior margin of the middle of the cleithrum beneath the gill cover in 12 or 13 mm larvae.

In the tail region the ventral midline melanophores gradually become embedded, anterior ones first, and are obscured by overlying musculature by the time larvae are 13 mm long. A melanophore is sometimes present near the tip of the notochord.

The pigmentation of the paired fins increases in intensity throughout the larval period, although the distal base of the pectoral fin remains unpigmented. As the pelvic fins develop, melanophores line the rays giving a striated appearance similar to that of the pectoral fins.

Melanophores appear on the anterior portion of the spinous dorsal fin by the time larvae are 11 mm long, and the anterior two-thirds of the fin remains rather heavily pigmented throughout larval development. The soft dorsal and anal fins remain unpigmented.

One to several internal, vertically elongate melanophores appear at the base of the caudal fin posterior to the hypural elements on most larvae >9 mm long, but the fin base is never completely lined with pigment.

During the transformation period, 16 to 21 mm, pelagic juvenile pigmentation begins to develop. On the head, pigment increases around the posttemporal spines and joins with the nape pigment. Internal and external melanophores are added on the dorsal part of the opercle forming a patch which expands ventrally on specimens >19 mm. Scattered melanophores appear along the dorsal surface of the snout and the anterior portion of the upper lip (internal and external) on specimens >18.5 mm long. Pigment increases around the orbit, lining the dorsal, posterior, and ventral margin of the orbit by 19 mm. In the abdominal region, an increase in musculature over the gut cavity obscures the internal gut pigment although scattered external melanophores persist. The nape patch extends anteriorly joining the head pigment, laterally toward the body midline, and posteriorly to the 12th dorsal spine. Two saddles of intensified melanistic pigment begin to develop beneath the first dorsal fin late in the transformation period. An anterior saddle joins the head pigment and another saddle located midfin expands ventrolaterally. Melanophores are added dorsally and ventrally along the anterior margin of the cleithrum beneath the gill cover, eventually appearing as a line of pigment. In the tail region, melanophores appear beneath the middle of the second dorsal fin in 16 mm specimens. They expand anteriorly to join the pigment beneath the spinous dorsal, posteriorly over the caudal peduncle, and laterally towards the body midline appearing as a saddle by 20 mm. Some melanophores at the base of the second dorsal fin become concentrated along muscles surrounding the dorsal pterygiophores giving the appearance of vertical lines of pigment by 20 mm. An additional melanophore may appear at the point of articulation of each dorsal soft ray 4 through 10 beginning on 18 mm specimens. Pigment is added internally and externally along the lateral midline of the caudal peduncle. On the first dorsal fin pigmentation increases extending posteriorly to the 11th or 12th dorsal spine.

In pelagic juveniles >22 mm long, small melanophores appear over the surface of the head. Melanophores almost entirely ring the orbit by 31 mm. Pigment increases on the snout and upper and lower jaws. The two pigment saddles beneath the first dorsal fin become more pronounced and extend more ventrolaterally. A third saddle forms beneath the first dorsal fin posterior to the first two in specimens about 22 to 25 mm long. In the tail region, the saddle beneath the second dorsal fin extends to the lateral midline by 24 mm and eventually reaches the ventral body margin in a 57 mm specimen. The number of melanophores increases on the caudal peduncle until dorsal and lateral pigment are joined forming a fifth pigment saddle in juveniles about 25 mm long. This fifth saddle eventually extends to the ventral body margin as does the saddle beneath the spinous dorsal fin. An increase in the number of melanophores occurs along the lateral midline of the caudal peduncle giving the appearance of a distinguishable, but not heavy, line of pigment. Small melanophores are added between saddles 3 and 4 and 4 and 5, along the myosepta first. The pectoral and pelvic fins remain heavily pigmented, although the amount of pigment on the base of the rayed portion of the pectoral fin decreases. Pigmentation on the spinous dorsal fin decreases in intensity between spines III and V, and between spines VIII and IX, corresponding to areas between the first, second, and third pigment saddles on the body. On specimens >38 mm long, pigment on the dorsal fin

above the third saddle darkens into a distinct black blotch. Melanophores are added to the basal half of the second dorsal fin above the fourth saddle, appearing continuous with it on specimens >29 mm long. Melanophores are also added to the basal half of the anal fin eventually extending from the second anal spine to the posteriormost anal fin ray on all specimens >38 mm. Specimens >36 mm have a melanophore at the point of articulation of each soft anal fin ray, although these melanophores soon become obscured by musculature and scales. Three to seven small external melanophores are added near the bases of the caudal fin rays forming an indistinct line.

Benthic juveniles >60 mm long retain essentially the same melanistic pigment pattern as pelagic juveniles except the intensity decreases resulting in a somewhat faded appearance. Additional light scatterings of melanophores appear in the lower jaw and gular region, second dorsal and anal fins, and body in general. Two bars of pigment radiate ventrally from the posteroventral margin of the eye. The basic banding pattern and black blotch at the base of the dorsal fin remain evident in the largest juvenile, 130 mm, examined. This is the same banding pattern apparent in adults, however, the black blotch on the spinous dorsal fin disappears.

In life (Moser[8]) a juvenile (122 mm) is reddish-brown dorsally, with white on the belly and five brownish bars on the body. The first four bars extend ventrally to slightly below the lateral line and dorsally onto the dorsal fins as diffuse dark areas. The head is reddish-brown and pale below eye level, with three brownish transverse bars: one at the anterior level of the orbit, one at the posterior level of the orbit, and one between and posterior to the parietal ridges. A large spot is on the opercle dorsally, and the axillary region has a dusky blotch. Except for the dark bars, the first and second dorsal fins are dusky at the base, grading to pale orange or yellowish with vermillion or deep red at the margin. The basal half of the anal and pelvic fins is whitish and the distal half grades from reddish to dark orange-red at the tips. The outer pelvic ray has a milky white lateral margin. The pectorals and caudal fins are pale orange, the pectorals with dark orange-red tips and the caudal with a faint dusky band on its posterior half.

Occurrence (Figures 5, 6).—*Sebastes crameri* ranges from Santa Catalina Island off southern California to the Bering Sea (Miller and Lea 1972). Off Oregon, Washington, and British Columbia it is primarily an outer shelf/upper slope species generally occuring in depths of 150 to 300 m (Snytko and Fadeev 1974). Distinct population clumps have been found off the Oregon coast between lat. 44°30′ and 45°20′ N (Snytko and Fadeev 1974). Most of our collections containing young *S. crameri* were taken along a transect off Newport (lat. 44°39.1′ N) off the central Oregon coast. The smallest larvae and the greatest numbers of larvae and pelagic juveniles were taken at stations 83 and 93 km offshore (water depths 700-1,300 m). The nearest inshore station on this transect at

[8]H. G. Moser, Fishery Biologist (Research), Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. 1977.

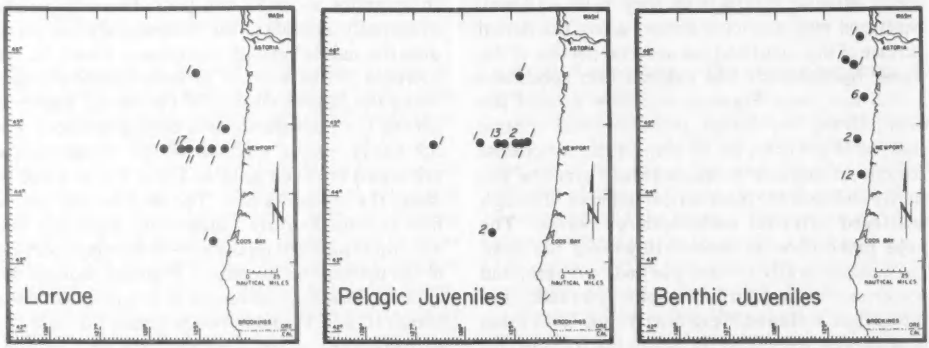

FIGURE 5.—Number of specimens and location of capture of larvae and juveniles of *Sebastes crameri* off Oregon (1961-75) described in this paper.

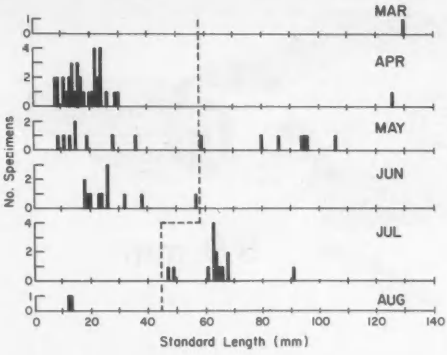

FIGURE 6.—Seasonal occurrence of larvae and juveniles of *Sebastes crameri* off Oregon. Data from 1961 to 1975 combined. Dashed line separates pelagic and benthic stages.

which a larva (15.7 mm) was taken was 28 km (depth 95 m). The farthest offshore occurrence on this transect was a 26 mm pelagic juvenile 194 km offshore. Benthic juveniles were generally taken nearer to shore than larvae or pelagic juveniles at depths of 55 to 200 m. Most pelagic specimens came from Isaacs-Kidd midwater trawls towed obliquely through the water column. Four specimens, 17.7, 24.0, 38.2, and 56.9 mm, were collected in a neuston net in June, 56 to 65 km off Newport.

Spawning times reported for *S. crameri* are November through March off California (Phillips 1964) and primarily February off Oregon, Washington, and British Columbia (Westrheim 1975; Westrheim et al. see footnote 7). However, mature females with ovaries containing embryos have been collected in February, March, April, and June (Westrheim et al.,[9] see footnote 7; Harling et al.[10]). Pelagic specimens in our collections were taken primarily in April, May, and June although two postflexion larvae were taken in August. Larvae under 10 mm were only taken in April and May. No specimens were taken September through February. Because of a lack of information on larval growth, parturition time cannot be inferred. The wide range of lengths of pelagic specimens, 8 to 30 mm in April, 9 to 36 mm in May, 18 to 57 mm in July, indicates spawning may be variable and protracted. Benthic juveniles were taken March through July.

In trawl surveys off Oregon, adults ranked second in biomass only to *S. diploproa* of all rockfishes collected over the continental slope and fifth or sixth on the continental shelf (Demory et al. 1976). Snytko and Fadeev (1974) reported it to be one of the most abundant trawl-caught rockfish species over the slope together with *S. alutus*, *S. saxicola*, and *S. diploproa*. This species was one of the three major contributors to the 1963-71 Oregon landings of the Pacific ocean perch fishery exceeding *S. alutus* in 1971 (Niska 1976). Although little can be said about the actual abundance of larvae and juveniles off Oregon because of the various kinds of samples examined and irregular nature of the sampling effort, they were one of the more common kinds relative to the other species of *Sebastes* in the samples.

SEBASTES PINNIGER (GILL) (Figures 7, 8, 9)

Literature.—Pigmentation of preextrusion larvae of *S. pinniger* was listed in tabular form by Westrheim (1975). Newborn to 2-wk-old larvae were described by Waldron (1968) and the older larva was redrawn by Moser et al. (1977). Mean length of larvae at hatching is 3.6 mm SL. Newborn larvae have an irregular double row of pigment (usually <16 melanophores) along the ventral midline between the 18th and 22d myomere and some pigment above the yolk sac near the anus. After 2 wk additional melanophores are present at the tip of the lower jaw, on the ventral part of the yolk sac, on the pectoral fins, along the dorsal midline in an irregular double row between the 19th and 21st myomeres, and in the hypural region. The ventral midline melanophores may extend as far forward as the 14th myomere.

Identification (Table 7, Appendix Tables 2-6).—A total of 269 specimens of *S. pinniger*, 7.9 to 181 mm long, were identified. Juveniles were identified using the following combination of characters compiled from specimens in our collections:

Gill rakers = 40-45, left arch; 38-46, right arch
Lateral line pores = 40-45
Pectoral fin rays = 16-18, usually 17

[9]Westrheim, S. J., W. R. Harling, D. Davenport, and M. S. Smith. 1968. Preliminary report on maturity, spawning season, and larval identification of rockfishes (*Sebastodes*) collected off British Columbia in 1968. Fish. Res. Board Can., Manuscr. Rep. 1005, 28 p.

[10]Harling, W. R., M. S. Smith, and N. A. Webb. 1971. Preliminary report on maturity, spawning season, and larval identification of rockfishes (Scorpaenidae) collected during 1970. Fish. Res. Board Can. Manuscr. Rep. 1137, 26 p.

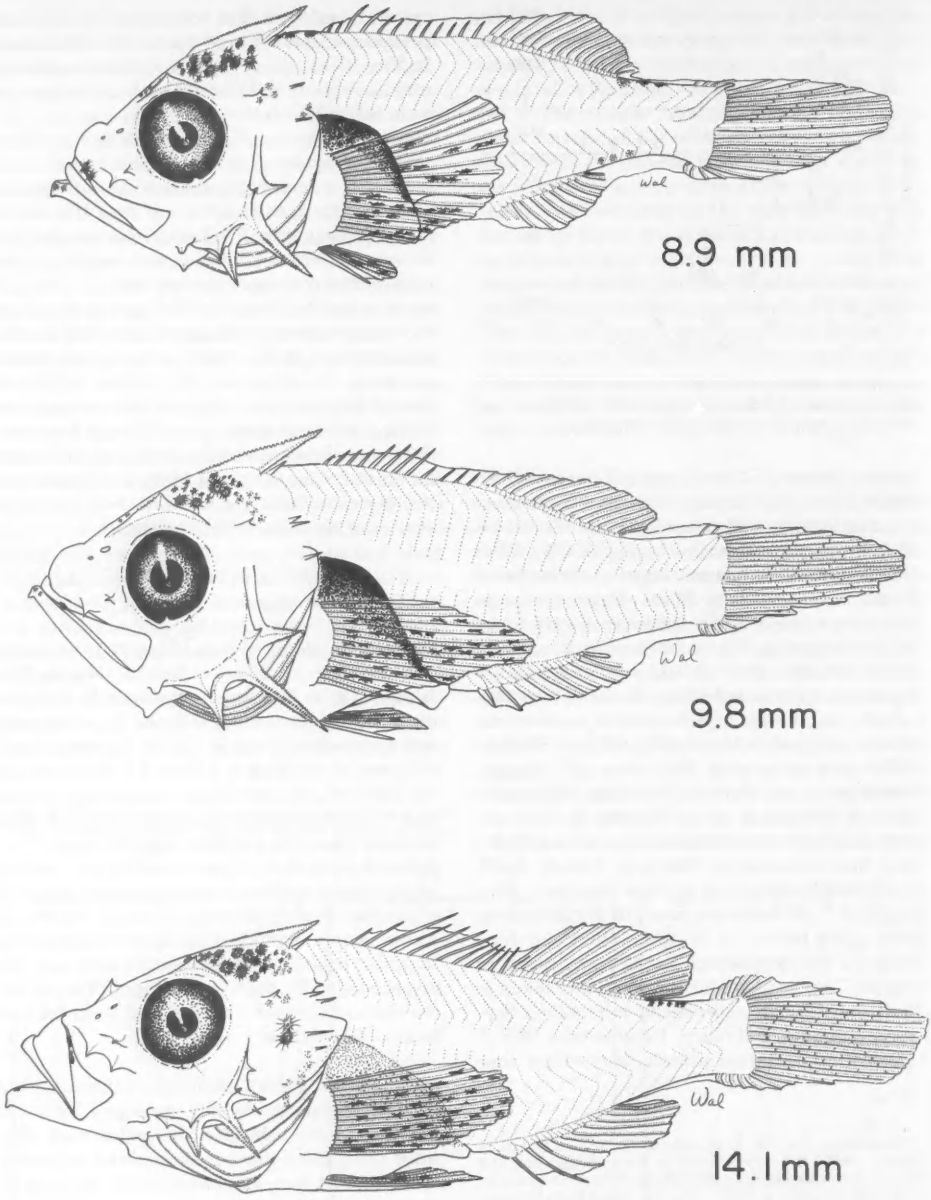

FIGURE 7.—Planktonic larvae (8.9, 9.8 mm) and transforming specimen (14.1 mm) of *Sebastes pinniger*.

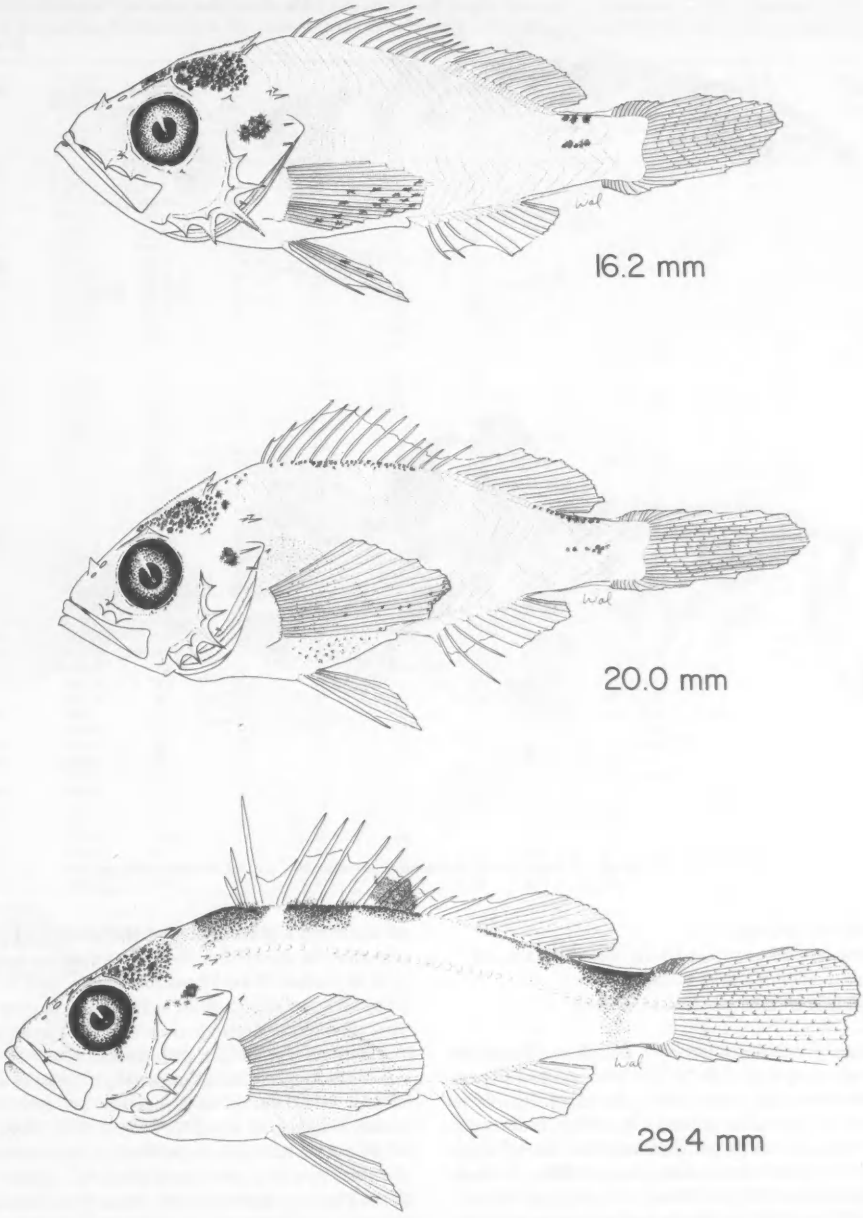

FIGURE 8.—Transforming specimen (16.2 mm) and pelagic juveniles (20.0, 29.4 mm) of *Sebastes pinniger*.

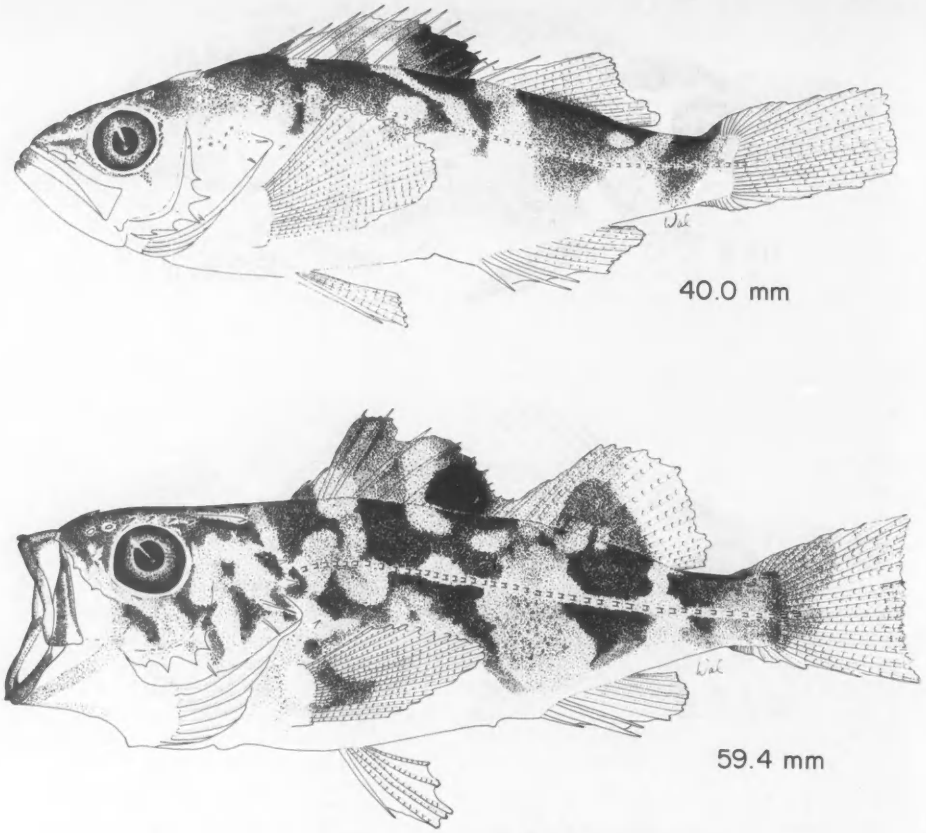

FIGURE 9.—Pelagic juvenile (40.0 mm) and benthic juvenile (59.4 mm) of *Sebastes pinniger*.

Anal fin soft rays = 7
Dorsal fin soft rays = 13-15, usually 14 or 15
Supraocular spine = present
Interorbital space = flat to convex.

Large juveniles (>26 mm SL) have the black blotch at the base of the posterior half of the spinous dorsal fin characteristic of adults. Other *Sebastes* juveniles which have a black blotch, e.g., *S. melanops*, *S. flavidus*, *S. crameri*, do not agree with the characters given above. Of the *Sebastes* species occurring off Oregon, *S. pinniger* has the best fit to all these characters. *Sebastes miniatus* and *S. emphaeus* also agree with many of the counts. However, juvenile *S. miniatus* and *S. emphaeus* lack a black blotch at the posterior base of the spinous dorsal fin. *Sebastes miniatus* usually has 18 rather than 17 pectoral rays, and *S. emphaeus* lacks supraocular spines. The larvae and juveniles in the series in question were among the most abundant in our collections. Adult *S. pinniger* are known to be abundant in trawlable areas offshore whereas *S. miniatus* are not commonly taken (Demory et al. 1976; Niska 1976). *Sebastes emphaeus*, although not previously reported from Oregon, is well represented in our samples. Pigment pattern, general body shape, time of occurrence, and constancy in number of anal fin soft rays and pectoral rays helped link the developmental series together.

TABLE 7.—Meristics from larvae and juveniles of *Sebastes pinniger* off Oregon, based on unstained specimens. Specimens above dashed line are undergoing notochord flexion. All specimens had 8 superior and 7 inferior principal caudal fin rays and 7 branchiostegal rays on each side.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Pelvic fin spines and rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows
			Left	Right	Left	Right	Left	Right	Left	Right	
7.8	(1)	(1)	—	17	(1)	(1)	—	—	—	—	—
7.8	(1)	(2)	17	—	I,(1)	I,(1)	—	—	—	—	—
8.8	VIII+I,14	III,7	17	17	I,5	I,5	—	—	—	—	—
8.9	IX+I,15	III,7	17	17	I,5	I,5	—	—	—	—	—
9.3	XIII,14	III,7	18	17	I,5	I,5	—	—	—	—	—
9.8	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
10.7	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
10.7	XIII,15	III,7	17	17	I,5	I,5	—	—	—	—	—
10.9	XIII,15	III,7	17	17	I,5	I,5	—	—	—	—	—
12.3	XIII,15	III,7	17	17	I,5	I,5	—	—	—	—	—
12.3	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
[4]12.8	XIII,15	III,7	17	17	I,5	I,5	—	—	—	—	—
[4]13.0	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
[4]14.1	XIII,14	III,7	17	17	I,5	I,5	—	27+ 12 or 13 = 39 or 40	—	—	—
[4]14.2	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
[4]15.2	XIII,15	III,7	17	17	I,5	I,5	—	—	—	—	
[4]16.0	XIII,14	III,7	17	17	I,5	I,5	—	28+13=41	—	—	—
[4]16.0	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
[4]16.2	XIII,15	III,7	17	17	I,5	I,5	—	27+13=40	—	—	—
[4]16.8	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
[4]17.8	XIII,15	III,7	18	18	I,5	I,5	—	27+12=39	—	—	—
[4]18.4	XIII,14	III,7	17	17	I,5	I,5	—	—	—	—	—
[5]18.6	XIII,15	III,7	17	18	I,5	I,5	27+14=41	28+14=42	—	—	—
[5]18.9	XIII,15	III,7	17	17	I,5	I,5	29+13=42	28+13=41	—	—	—
[5]19.4	XIII,15	III,7	17	17	I,5	I,5	27+13=40	26+12=38	—	—	—
[5]19.5	XIII,14	III,7	18	18	I,5	I,5	27+13=40	27+12=39	—	—	—
[5]20.0	XIII,14	III,7	17	17	I,5	I,5	27+14=41	28+13=41	44	—	—
[5]20.8	XIII,14	III,7	17	17	I,5	I,5	28+13=41	28+13=41	—	—	—
[5]22.4	XIII,14	III,7	17	18	I,5	I,5	28+13=41	29+13=42	—	≈44	—
[5]23.4	XIII,14	III,7	17	17	I,5	I,5	29+13=42	28+14=42	≈44	—	—
[5]26.4	XIII,14	III,7	17	17	I,5	I,5	29+15=44	29+14=43	≈43	≈40	—
[5]26.4	XIII,14	III,7	17	17	I,5	I,5	28+14=42	28+13=41	—	—	—
[5]26.6	XIII,15	III,7	17	17	I,5	I,5	28+13=41	29+14=43	—	—	—
[5]28.6	XIII,14	III,7	17	17	I,5	I,5	28+13=41	29+14=43	≈42	≈44-45	—
[5]28.8	XIII,15	III,7	17	17	I,5	I,5	29+13=42	28+13=41	—	—	—
[5]29.4	XIII,14	III,7	17	17	I,5	I,5	28+13=41	28+14=42	≈44	—	—
[5]30.4	XIII,13	III,7	17	17	I,5	I,5	28+13=41	28+13=41	≈44	—	—
[5]30.9	XIII,14	III,7	17	18	I,5	I,5	31+14=45	31+15=46	—	—	—
[5]34.1	XIII,14	III,7	16	17	I,5	I,5	29+14=43	29+14=43	≈44	≈44	—
[5]38.0	XIII,14	III,7	17	18	I,5	I,5	28+14=42	29+14=43	—	≈42	—
[5]38.7	XIII,15	III,7	17	17	I,5	I,5	27+13=40	29+13=42	≈42	≈44	—
[5]39.2	XIII,14	III,7	17	17	I,5	I,5	29+14=43	29+14=43	≈41	≈41	—
[5]40.0	XIII,14	III,7	17	17	I,5	I,5	28+14=42	29+13=42	≈40	—	—
[5]41.0	XIII,14	III,7	17	17	I,5	I,5	30+14=44	30+14=44	—	43	—
[5]42.4	XIII,15	III,7	17	17	I,5	I,5	29+14=43	29+14=43	40	40	—
[6]59.4	XIII,14	III,7	17	18	I,5	I,5	29+14=43	29+14=43	40	43	≈51
[6]117.7	XIII,14	III,7	17	17	I,5	I,5	29+14=43	29+13=42	45	44	—
[6]181	XIII,15	III,7	17	17	I,5	I,5	30+14=44	28+14=42	43	43	≈50

[1]Forming.
[2]Not formed.
[3]Posteriormost dorsal or anal spine appears as a soft ray.
[4]Transforming.
[5]Pelagic juvenile.
[6]Benthic juvenile.

Distinguishing Features.—Characters useful in distinguishing the smallest larvae (7.8 mm) of *S. pinniger* identified from our collections are the presence of remnants of both dorsal and ventral midline melanophores the anterior of which are internal, the lightly pigmented pectoral fins, melanophores at the tip of the lower jaw and on the anteroventral margin of the maxillary, the presence of one or two large external stellate melanophores on the dorsum just posterior to the parietal spines, the relatively deep body (40% SL), long parietal spines (24% HL), and long pectoral fins (25% SL). Later stage larvae are characterized by their relative lack of pigment on the trunk except over the gut, together with the relatively deep body and long parietal and third posterior preopercular spines. Meristics, presence of the supraocular spine, flat to convex shape of the interorbital space, and dark blotch at the base of the spinous dorsal serve to distinguish the juveniles.

General Development.—The smallest larvae of *S. pinniger* identified, 7.8 mm, are in the final stage of notochord flexion. By the time larvae are 8.8 mm long, flexion is complete. Transformation to pelagic juvenile begins in larvae >12.5 mm long with the initiation of spine formation in the dorsal and anal fin "prespines" and the appearance of a patch of melanophores on the dorsum immediately posterior to the second dorsal fin. Transformation of the "prespines" to spines is complete in specimens >18.6 mm and some pigment has been added beneath the first dorsal fin marking the beginning of pelagic juvenile pigmentation. The dorsal pigmentation becomes more pronounced during the pelagic juvenile period which lasts until ≈40 to 50 mm. The largest pelagic juvenile taken was 42.4 mm and the smallest benthic juvenile was 59.4 mm.

Morphology (Tables 4, 8).—Forty-eight specimens of *S. pinniger*, 7.8 to 181.0 mm long, were measured for developmental morphology. Larvae appear quite deep bodied, but body depth at the pectoral fin base decreases considerably during the pelagic period from 40 to 33% SL. In comparison, body depth at the anus/SL changes relatively little, decreasing slightly then increasing. Snout to anus length increases from 59 to 64% SL while snout to pelvic fin distance increases to a lesser degree.

Head length decreases from 43 to 37% SL during development as more marked changes occur in eye diameter, decreasing from 37-39 to 27% HL, and interorbital distance, decreasing from 37 to 20% HL. Upper jaw length/HL first decreases and then increases while snout length/HL increases then decreases. The length of the angle gill raker increases with respect to head length from 11 to 14 or 15%.

Larvae and young juveniles up to 24 mm have a prominent symphyseal knob directed anteroventrally. It becomes less obvious with development and is barely noticeable by the time juveniles are 29 mm long.

Fin Development (Tables 4, 7, 8).—Pectoral fins are present and the adult complement of 16 to 18 (usually 17) rays can be counted in 7.8 mm larvae of *S. pinniger*, although the ventral rays are not fully formed until >8 mm. The pectoral fins are relatively long in flexion and postflexion larvae averaging 25% SL and they maintain this approximate proportion through development. Depth of the pectoral fin base decreases from 15 to 9% SL.

Developing pelvic fins are visible on 7.8 mm larvae and the adult complement of I, 5 is countable in postflexion larvae of 8.8 mm. The pelvic fins are rather long, averaging 14% SL in flexion larvae and increasing to a maximum of 23% SL in transforming specimens. Length of the pelvic spine, always less than the fin itself, increases from 5% SL in flexion larvae to 20% in transforming specimens then decreases to 13% in benthic juveniles.

The adult complement of principal caudal rays can be counted in 7.8 mm larvae, before the completion of notochord flexion at 8.8 mm. Counts of secondary caudal rays were 11 superior and 12 inferior rays on each of two stained juveniles, 29.5 and 33.4 mm.

Bases of some of the dorsal and anal fin ray and spine elements are visible on the 7.8 mm larvae. The adult complement of ray and spine elements is present in postflexion larvae >9 mm and the rays and spines (with "prespines") appear fully formed by 9.3 mm. Transformation of "prespines" to spines is completed by 18.5 mm. The longest dorsal spine increases from 20 to 38% HL during the pelagic period. The longest dorsal ray increases from 32 to 42 or 43%. The longest anal spine increases from 19 to 37% HL during pelagic development.

Spination (Tables 4, 9).—Spines present on the left side of the head of the two smallest specimens of *S. pinniger*, 7.8 mm, include the parietal; the nuchal; the first and third anterior preopercular; the second, third, and fourth posterior preopercular; the postocular, the pterotic, the inferior posttemporal; the first spine of the inferior infraorbital series; and the first spine of the superior infraorbital series.

The parietal spine and ridge are heavily and relatively deeply serrated in small larvae and the spine is relatively long, averaging 24% HL in flexion larvae. Its relative length decreases with development to 20% HL in flexion larvae, 10% in transforming specimens, and 7% in early pelagic juveniles, <20 mm. The much smaller nuchal spine averages 4 or 5% HL in postflexion and transforming larvae, decreasing to 1% in benthic juveniles. The parietal and nuchal spines fuse together, beginning in pelagic juveniles >20 mm until only the nuchal tip is visible in juveniles >40 mm. Serrations along the parietal ridge can be seen on specimens up to 39 mm.

TABLE 8.—Measurements (millimeters) of larvae and juveniles of *Sebastes pinniger* from waters off Oregon. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle	gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
7.8	9.8	4.6	3.3	0.88	1.6	1.2	1.2	3.2	2.1	2.1	1.1	0.40	1.2	3.4	0.80	[4]	1.2	—	[5]	[6]	[6]
7.8	9.5	4.5	3.4	0.92	1.6	1.3	1.3	3.1	2.2	1.8	1.2	[5]	0.96	3.0	0.84	[4]	1.1	—	[5]	[6]	[6]
8.8	11.2	5.5	4.2	1.0	2.2	1.5	1.4	3.7	2.5	2.1	1.2	0.72	0.88	3.6	—	—	1.2	—	—	1.0	[6]
8.9	11.1	4.6	3.4	0.92	1.4	1.4	1.3	3.0	2.2	1.8	1.2	0.88	1.1	3.4	0.76	0.16	1.2	—	0.46	1.1	[6]
9.3	11.5	5.6	4.0	1.3	1.9	1.5	1.4	3.5	2.6	2.1	1.2	1.2	1.4	3.8	0.94	0.10	1.4	—	0.52	1.1	[6]
9.8	12.3	5.8	4.1	1.2	1.9	1.6	1.5	3.8	3.0	2.7	1.2	—	1.7	3.4	0.96	0.18	1.6	0.34	—	1.3	0.60
10.7	14.1	6.6	4.7	1.3	2.2	1.9	1.6	4.3	3.2	2.7	1.4	—	1.9	4.8	—	—	—	0.54	1.1	1.5	1.0
10.7	13.4	6.3	4.6	1.6	2.0	1.9	1.4	3.9	2.9	2.7	1.3	1.6	2.3	4.7	—	—	1.2	0.48	1.0	1.4	0.88
10.9	12.8	6.3	4.5	1.2	2.2	1.8	1.5	4.3	3.3	—	1.4	1.6	2.0	4.4	—	—	1.5	0.44	0.92	1.4	0.84
12.3	15.5	7.7	5.0	1.3	2.1	1.9	1.7	4.4	3.4	3.0	1.4	—	2.4	4.9	0.44	0.18	1.6	0.56	—	1.9	1.0
12.3	15.4	7.6	5.2	1.6	—	2.1	1.7	4.8	3.7	3.5	1.4	—	2.8	5.2	—	0.36	1.3	0.64	1.5	1.9	—
[7]12.8	15.7	8.0	5.2	1.9	2.1	2.0	1.6	4.5	3.4	2.9	1.3	2.4	2.7	5.9	0.66	0.18	1.3	0.70	1.5	1.6	1.3
[7]13.0	15.2	8.2	5.5	1.7	2.1	2.1	1.6	4.8	3.5	3.5	1.5	—	2.7	5.9	0.60	0.30	1.6	0.68	1.3	2.0	1.1
[7]14.1	17.1	8.5	5.9	2.1	2.1	2.2	1.7	4.9	3.5	—	1.5	2.6	3.0	6.0	0.68	0.32	1.3	0.68	—	—	1.5
[7]14.2	16.8	8.6	5.7	1.6	—	2.2	1.8	5.1	3.9	—	1.6	2.5	3.0	5.8	—	0.36	1.3	0.72	1.7	2.2	1.5
[7]15.2	19.2	9.1	6.2	1.9	2.8	2.3	2.0	5.4	4.3	4.3	1.7	3.1	3.7	6.2	0.80	0.40	1.5	0.84	1.9	2.4	1.8
[7]16.0	20.0	9.4	6.2	1.7	2.8	2.4	2.0	5.9	4.5	4.5	1.8	—	3.8	6.2	—	0.28	1.4	0.80	2.4	—	2.0
[7]16.0	20.8	9.3	6.6	1.7	3.1	2.5	2.0	5.7	4.5	4.5	1.6	—	—	6.2	0.26	0.18	1.4	0.88	—	2.4	1.7
[7]16.2	20.6	10.2	6.9	1.9	3.2	2.6	2.0	6.2	5.0	5.1	1.8	—	4.1	6.7	—	0.50	1.6	0.90	2.8	2.9	—
[7]16.8	19.7	10.1	6.7	2.1	2.8	2.5	1.9	6.3	4.7	4.5	1.8	—	—	6.5	—	0.34	1.6	0.88	2.2	2.5	—
[7]17.8	20.8	10.7	7.0	2.2	2.8	2.7	2.0	6.4	5.2	4.8	1.8	3.6	4.1	7.6	—	—	1.6	0.90	—	2.8	—
[7]18.4	21.8	10.7	7.0	1.9	2.8	2.5	2.2	6.4	5.1	4.4	2.0	4.0	4.4	7.5	0.72	0.16	1.6	0.94	—	3.0	2.7
[8]18.6	22.9	11.7	7.6	2.3	3.3	2.6	2.0	6.2	4.7	5.0	1.8	3.6	4.2	8.6	0.70	0.32	—	1.1	2.6	3.2	2.6
[8]18.9	23.5	11.7	7.7	2.4	3.3	2.7	2.1	6.4	4.8	—	1.9	3.6	4.1	8.4	—	—	1.6	0.9	—	—	2.4
[8]19.4	23.4	11.2	8.0	1.9	3.4	2.7	2.2	6.6	5.4	5.2	1.9	4.2	4.6	7.6	0.46	0.30	1.7	1.1	—	3.1	2.6
[8]19.5	24.6	11.5	8.2	2.2	3.5	2.8	2.2	6.7	5.2	—	2.0	4.3	4.6	6.6	0.84	0.44	1.4	1.0	3.0	—	2.7
[8]20.0	25.4	11.5	7.4	1.8	3.4	2.8	2.2	7.4	5.6	5.7	2.0	—	4.6	8.0	0.40	0.30	—	1.1	—	3.2	2.8
[8]20.8	24.8	12.6	8.0	2.6	3.1	2.8	2.1	7.0	5.3	5.9	2.0	3.9	4.2	8.5	Joined	0.32	1.2	1.2	—	—	2.7
[8]22.4	26.7	13.0	8.4	2.0	3.4	3.0	2.3	7.7	5.9	6.0	2.2	4.5	5.2	8.0	Joined	0.26	1.4	1.2	—	—	3.2
[8]23.4	28.8	13.1	7.8	2.1	3.7	3.3	2.4	8.0	6.3	6.1	2.1	4.7	5.1	7.7	Joined	0.28	—	1.2	3.6	3.8	3.3
[8]26.4	33.4	15.2	9.1	2.1	4.2	3.5	2.6	8.9	7.0	7.3	2.5	—	6.0	9.9	Joined	0.40	1.4	1.5	—	4.0	4.0
[8]26.4	31.2	17.3	10.4	3.4	4.0	3.4	2.4	8.9	7.0	7.2	2.4	4.6	5.5	12.0	Joined	0.20	1.2	1.5	—	—	3.2
[8]26.6	32.0	17.0	10.6	2.6	4.2	3.4	2.2	8.9	7.1	7.1	2.4	4.8	6.1	10.9	Joined	0.40	—	1.4	—	—	3.6
[8]28.6	38.1	17.9	10.7	3.0	4.0	3.5	2.7	9.2	7.3	7.6	2.6	—	6.4	11.4	Joined	0.28	1.3	1.5	—	4.2	4.1
[8]28.8	36.3	19.2	10.6	3.4	4.3	3.7	2.6	9.6	7.6	7.6	2.6	5.2	6.2	13.1	Joined	0.30	1.2	1.5	4.0	4.1	4.4
[8]29.4	37.1	17.9	10.1	2.6	4.1	3.7	2.7	10.5	8.0	7.5	2.8	5.2	6.6	10.7	Joined	0.28	1.2	1.6	4.4	4.4	4.4
[8]30.4	38.1	20.5	11.5	3.7	4.9	3.7	2.6	10.1	7.5	7.7	2.5	5.2	6.5	13.4	Joined	—	1.2	1.6	4.4	4.4	4.4
[8]30.9	38.6	20.8	13.0	4.1	4.5	4.0	2.7	10.4	8.1	8.6	2.8	5.5	7.2	13.4	Joined	—	1.2	1.6	4.6	4.6	—
[8]34.1	42.6	22.7	12.5	3.9	5.3	4.0	2.7	11.0	8.3	—	2.8	5.7	6.6	15.5	Joined	0.34	1.5	1.6	4.4	4.8	4.8
[8]38.0	46.6	22.5	13.8	3.0	5.7	4.7	3.0	11.5	9.1	9.3	3.1	—	7.7	14.1	Joined	0.30	1.3	1.9	4.9	5.7	5.3
[8]38.7	46.4	23.4	13.3	3.3	6.0	4.5	2.9	12.0	9.8	9.6	3.4	6.6	7.8	14.2	Joined	0.46	1.4	2.1	5.4	—	—
[8]39.2	48.8	23.5	13.9	3.2	5.9	4.5	3.0	11.7	10.1	10.2	3.3	5.7	8.0	14.6	Joined	0.30	1.3	1.9	—	6.1	5.3
[8]40.0	49.1	23.5	14.9	3.6	6.0	4.7	3.3	12.5	10.4	9.6	3.6	6.5	8.8	15.5	Joined	0.30	1.4	2.1	5.3	6.6	6.3
[8]41.0	50.4	25.0	14.7	4.3	5.9	4.6	3.1	12.2	9.8	10.4	3.4	6.3	8.4	17.8	Joined	0.30	1.5	2.1	5.6	6.6	5.5
[8]42.4	51.7	26.4	15.4	4.3	5.7	4.9	3.0	13.0	11.0	10.2	3.7	6.4	8.7	16.5	Joined	0.40	1.4	2.1	5.1	6.3	5.2
[8]59.4	71.0	36.0	21.8	6.4	9.3	6.6	4.0	19.4	16.2	13.6	5.1	7.4	11.3	24.4	Joined	0.46	1.4	3.0	7.4	8.9	7.5
[9]117.7	141.8	78.3	43.8	12.5	19.5	11.2	8.6	41.6	33.2	29.4	10.1	14.8	25.5	48.3	Joined	0.64	1.7	6.6	13.8	17.4	14.2
[9]181	224	117.2	65.4	18.1	30.6	15.9	13.7	67.2	61.5	45.1	16.3	21.8	41.2	83.5	Joined	0.70	2.3	10.6	26.7	30.9	23.9

[1]Usually third or fourth in larvae, fifth or sixth in juveniles.
[2]Usually midfin.
[3]The second spine.
[4]Bump.
[5]Not formed.
[6]Forming.
[7]Transforming.
[8]Pelagic juvenile.
[9]Benthic juvenile.

The posterior series of preopercular spines are prominent in *S. pinniger* larvae. The heavily serrated third spine is relatively long averaging 32 to 34% HL in flexion and postflexion larvae. Its relative length then decreases to 5% in benthic juveniles. All five spines of the series are present in larvae >10 mm. Serrations are visible on the second, third, and fourth spines until ≈29 mm. The first posterior preopercular spine is sometimes bifid in pelagic juveniles. The smaller first and third spines of the anterior preopercular series are also conspicuous on small larvae, but decrease in prominence until they are no longer visible in pelagic juveniles >26 mm. The second anterior preopercular spine never becomes apparent.

The superior opercular spine is present on larvae by 9 mm and the inferior opercular spine appears later in larvae ≈12 or 13 mm. Both spines are present on juveniles. An interopercular spine develops on the edge of the gill cover, usually in larvae >10 mm. A subopercular spine was not present on any of the specimens examined.

The ridge anterior to the postocular spine is heavily serrated and remains so until preocular spine formation. The preocular appears first as a bump in transforming larvae ≈16.0 mm long and develops into a spine in pelagic juveniles >19 mm.

Development of the supraocular follows a similar pattern appearing at about the same time as the preocular. Beneath the eye the fourth spine of the superior infraorbital series is present in larvae >9 mm and the third spine of this series is present in all larvae >13 mm. The second superior infraorbital spine never forms. All three superior infraorbital spines disappear by 43 mm. The second spine of the inferior infraorbital series is present on specimens >10 mm and the two spines in this series persist in juveniles. The third inferior infraorbital spine never develops. The nasal spine develops

TABLE 9.—Development of spines in the head region of *Sebastes pinniger* larvae and juveniles. Specimens above dashed line are undergoing notochord flexion. + denotes spine present and − denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
7.8	+	+	+	−	+	−	+	+	+	−	−	−	−	−	−	−	+
7.8	+	+	+	−	+	−	+	+	+	−	−	−	−	−	−	−	+
8.8	+	+	+	−	+	−	+	+	+	−	+	−	−	−	−	−	+
8.9	+	+	+	−	+	−	+	+	+	−	+	−	−	−	−	−	+
9.3	+	+	+	−	+	+	+	+	+	−	+	−	−	−	−	−	+
9.8	+	+	+	−	+	+	+	+	+	−	+	−	−	−	−	−	+
10.7	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
10.7	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
10.9	+	+	+	−	+	+	+	+	+	+	+	−	−	−	−	−	+
12.3	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
12.3	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[1]12.8	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+
[1]13.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+
[1]14.1	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[1]14.2	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[1]15.2	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[1]16.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[1]16.0	+	+	+	−	+	+	+	+	+	+	+	+	+	−	[2]	+	+
[1]16.2	+	+	+	−	+	+	+	+	+	+	+	+	+	−	[2]	[2]	+
[1]16.8	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+
[1]17.8	+	+	+	−	+	+	+	+	+	+	+	+	+	−	[2]	+	+
[1]18.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	[2]	+	+
[3]18.6	+	+	+	−	+	+[4]	+	+	+	+	+	+	+	−	[2]	[2]	[2]
[3]18.9	+	+	+	−	+	+[4]	+	+	+	+	+	+	+	−	[2]	[2]	[2]
[3]19.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	−	+
[3]19.5	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	+	+
[3]20.0	+	+	+	−	+	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]20.8	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	+	+
[3]22.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	+	+
[3]23.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	+	+
[3]26.4	+	+	+	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]26.4	+	+	+	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]26.6	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]28.6	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]28.8	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]29.4	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]30.4	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]30.9	+	+	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]34.1	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]38.0	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]38.7	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]39.2	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]40.0	+	+	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+
[3]41.0	+[5]	+[5]	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[3]42.4	+[5]	+[5]	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[6]59.4	+[5]	+[5]	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[6]117.7	+[5]	+[5]	−	−	−	+	+	+	+	+	+	+	+	−	+	+	+
[6]181	+[5]	+[5]	−	−	−	+[4]	+	+	+	+	+	+	+	−	+	+	+

[1]Transforming.
[2]Bump indicates beginning of spine formation.
[3]Pelagic juvenile.
[4]Spine is bifid.
[5]Parietal and nuchal spines fused.
[6]Benthic juvenile.
[7]Spine has become rounded, no sharp tip.

TABLE 9.—Continued.

Standard length (mm)	Infraorbitals							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
7.8	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
7.8	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.8	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.9	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
9.3	+	–	–	+	–	–	+	(2)	–	–	+	–	+	–	–
9.8	+	–	–	+	–	–	+	(2)	–	–	+	–	+	+	–
10.7	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
10.7	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
10.9	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.3	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
12.3	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[1]12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[1]13.0	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
[1]14.1	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]14.2	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
[1]15.2	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]16.0	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]16.0	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]16.2	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]16.8	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]17.8	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[1]18.4	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[3]18.6	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[3]18.9	+	+	–	+	–	+	+	+	–	–	+	+	+	+	–
[3]19.4	+	+	–	+	–	+	+	+	–	–	+	–	+	+	–
[3]19.5	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]20.0	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]20.8	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]22.4	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]23.4	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]26.4	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]26.4	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]26.6	+	+	–	+	–	(2)	(2)	+	–	–	+	+[4]	+	+	+
[3]28.6	+	+	–	+	–	+	+	+	–	–	+	+	+	+	+
[3]28.8	+	+	–	?	–	?	?	+	–	–	+	+	+	+	+
[3]29.4	+	+	–	(2)	–	(2)	–	+	–	–	+	+[4]	+	+	+
[3]30.4	+	+	–	–	–	–	–	+	–	–	+	+	+	+	+
[3]30.9	+	+	–	–	–	–	–	+	–	–	+	+	+	+	+
[3]34.1	+	+	–	–	–	–	–	+	–	–	+	+	+	+	+
[3]38.0	+	+	–	–	–	–	–	+	–	+	+	+	+	+	+
[3]38.7	+	+	–	–	–	–	–	+	–	+	+	+	+	+	+
[3]39.2	+	+	–	–	–	–	–	+	–	+	+	+	+	+	+
[3]40.0	+	+	–	–	–	–	–	+	–	+	+	+	+	+	+
[3]41.0	+	+	–	–	–	–	–	+	–	+	+	+	+	+	+
[3]42.4	+	+	–	–	–	–	–	+	–	+	+	+	+	+	+
[5]59.4	+	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[5]117.7	+[7]	+	–	–	–	–	–	+	–	+	(2)	–	+	+	+
[5]181	+[7]	+	–	–	–	–	–	+	–	+	–	–	+	+	+

first as a bump in larvae >9 mm and is present in juveniles.

The tympanic spine appears on specimens >35 mm SL. This spine forms at the anterior edge of a foramen of the cephalic lateral line system. The pterotic spine, present in the smallest larvae, disappears in benthic juveniles. The supracleithral spine develops posterior to the inferior posttemporal on larvae >9.5 mm and the superior posttemporal spine is present dorsal to these in specimens >14 or 15 mm. This latter spine is occasionally bifid. The inferior posttemporal disappears in benthic juveniles. Posterior to the opercle the cleithral spine is visible in pelagic juveniles of 19.5 mm and persists in benthic juveniles.

Scale Formation.—Lateral line pores are visible on specimens >17 mm. Scale formation has begun on juveniles >23 mm.

Pigmentation.—The smallest larvae of *S. pinniger* examined, 7.8 mm (similar to the 8.9 mm specimen illustrated), have pigment on the head over the brain. Melanophores line the inner tip of the lower jaw and a few are present along the anteroventral margin of the maxillary. In the abdominal region, an internal melanistic shield covers the dorsal half of the gut, appearing darkest on the dorsal surface. A few additional melanophores are present along the ventral midline of the gut cavity. Two or three large stellate melanophores are

on the dorsum immediately posterior to the parietal spines. In the tail region several embedded melanophores, sometimes fused, are on the dorsal and ventral body midlines near the caudal peduncle. These midline melanophores are present in the same region as the midline pigment shown on Waldron's (1968) reared 2-wk-old larva. The pectoral fin blades are lightly pigmented with elongate melanophores. Melanophores are also present on the inner side of the pectoral fin base but not on the outer side. The pelvic fins also have a light scattering of melanophores. The caudal fin base is unpigmented.

During larval development, pigment increases on the head over the brain. Occasionally one or two melanophores are present on the snout. Melanophores lining the inner tip of the lower jaw and those on the anteroventral margin of the maxillary remain throughout the larval period.

The melanistic shield over the gut intensifies laterally and melanophores on the ventral midline disappear. The two to three stellate melanophores on the dorsum posterior to the parietal spines disappear by the time larvae are 9 mm long.

In the tail region, the dorsal and ventral midline melanophores near the caudal peduncle are no longer visible on larvae >9 mm.

The rayed portions of the pectoral and pelvic fins remain lightly pigmented during the larval period but melanophores are no longer present on the inner side of the pectoral fin base in larvae >10 mm.

During the transformation period, 12.8 to 18.6 mm, the amount of pigment increases gradually. In the head region, internal pigment is added to the opercle dorsally until a patch of 6 to 10 melanophores is visible on specimens >16 mm. Internal gut pigmentation decreases in intensity due to overgrowth by musculature. A few melanophores sometimes appear on the nape and beneath spines V to XI of the first doral fin, although not consistently until late in the transformation period in specimens >17 mm. The most prominent addition of pigment occurs dorsally in the tail region just posterior to the soft dorsal fin. Melanophores are added along the dorsolateral surface of the caudal peduncle. Directly below these melanophores, three or four internal and one to four external melanophores are added along the lateral midline in specimens >15 mm. The amount of pigment on the pectoral and pelvic fins decreases during this period.

During the pelagic juvenile period, 18.9 to 42.4 mm, new pigment is added over the dorsal surface of the head, interorbital, snout, premaxillary (specimen >26 mm), and on the lower jaw (specimen >35 mm). The opercular patch enlarges. Around the eye, melanophores are added first on the posteroventral margin of the orbit in specimens 19 to 23 mm, and eventually line the orbit. A radiating bar of melanophores begins to extend from the posteroventral margin of the orbit on specimens >28 mm, extending onto the preopercle on specimens >30 mm. In the abdominal region, melanophores are added dorsolaterally to the nape and beneath spines V to X of the first dorsal fin forming two pigment patches connected by a dorsal row of melanophores by 23 mm. The nape patch expands forming a saddle (first in position) extending from the parietal spine to the third dorsal spine and ventrally to the superior posttemporal spine by 28 mm. Two saddles (second and third) develop from the pigment patch beneath the spinous dorsal fin, midfin beneath spines IV to VI and posteriorly beneath spines VIII to XI. These two saddles are separated by a relatively unpigmented area on the dorsum. As they extend more ventrolaterally, they fuse together in two places just above and below the lateral line creating a second, circular, less pigmented area on specimens >39 mm. These two saddles eventually extend to the dorsal portion of the gut cavity by 42 mm. A single external melanophore may occur on the midanterior margin of the cleithrum beneath the gill cover. In the tail region, the dorsal patch of pigment on the caudal peduncle extends to the lateral line forming another saddle by 23 mm which reaches the ventral body margin by 27 mm. Beneath the second dorsal fin melanophores increase in number and become concentrated along the muscles surrounding the dorsal pterygiophores appearing as vertical lines of pigment by 23 mm. Melanophores also develop at the point of articulation of all but the anteriormost three or four dorsal soft rays. A melanistic saddle (fourth in position) develops beneath soft dorsal rays 3 to 12 or 13 extending ventrolaterally to the body midline by 34 mm and three-fourths the distance to the ventral margin by 42 mm. The pectoral and pelvic fins are no longer pigmented in specimens >21 mm. Pigment develops on the first dorsal fin membrane between spines IX and XI in juveniles >26 mm, eventually forming the "black blotch" characteristic of larger juveniles and adults. Melanistic bars form on the first dorsal fin between spines I to III

and V to VIII above the first and second saddles. By 39 mm the outer half of the fin is completely pigmented, while two unpigmented areas remain on the proximal half of the fin between the two pigment bars. Melanophores are added on the second dorsal fin above the fourth saddle until the proximal one-fourth of the fin between rays 2 and 13 or 14 is pigmented. The base of the caudal fin never becomes outlined with melanophores, but some melanophores develop on the dorsal secondary caudal rays.

Recently preserved pelagic juveniles of *S. pinniger*, 32 to 35 mm, are covered with orange chromatophores which are lost during prolonged preservation. They are present on the dorsal part of the head, on the snout, around the orbit, and on the opercle. On the body they are concentrated along the myosepta and lateral midline, with greater numbers on the dorsal half of the body but also extending to the ventral margin. Orange chromatophores are also concentrated on the spinous dorsal fin, along the basal one-fourth of the caudal fin, and the anal fin membrane around the anal spines.

A general increase in melanistic pigmentation occurs in benthic juveniles >59 mm. On the head, the two pigment bars beneath the orbit remain distinct and extend over the operculum. Pigment increases between the saddles obscuring the pattern seen on pelagic juveniles. Melanophores are added to both the inner and outer surfaces of the pectoral fin base and on the basal one-third of the pectoral fin blade. The pelvic fin remains unpigmented. The addition of melanophores to the spinous dorsal fin obscures the pattern seen on pelagic juveniles although the black blotch remains intense and distinct. The entire caudal fin is lightly pigmented with more intense pigment occurring over the bases of the primary rays and all upper secondary rays.

Occurrence (Figures 10, 11).—Adults of *S. pinniger* occur between Cape Colnett, Baja California, and southeast Alaska (lat. 56° N, long. 134° W) (Hart 1973). Off Oregon they are most common on the continental shelf between 100 and 200 m (Snytko and Fadeev 1974). A major population concentration has been found between lat. 44°30′ and 45° N off Oregon (Snytko and Fadeev 1974).

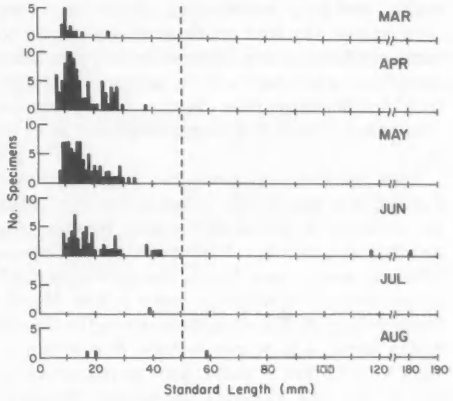

FIGURE 11.—Seasonal occurrence of larvae and juveniles of *Sebastes pinniger* off Oregon. Data from 1964 to 1975 combined. Dashed line separates pelagic and benthic stages.

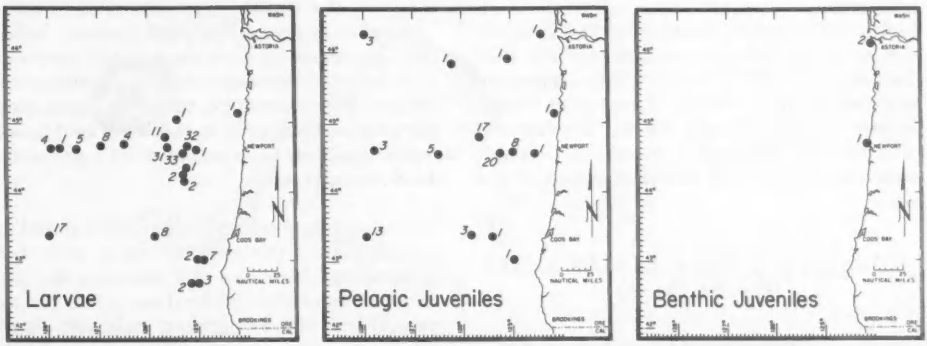

FIGURE 10.—Number of specimens and location of capture of larvae and juveniles of *Sebastes pinniger* off Oregon (1964-75) described in this paper.

Larvae, including transforming specimens, of *S. pinniger* in our collections were captured at a wide range of stations from 13 to 306 km offshore. The largest numbers and smallest larvae (<8.8 mm) were taken at stations 83 to 120 km off Newport beyond the continental shelf break. This may partly be a reflection of increased sampling effort in that area. Pelagic juveniles occurred at a similar wide range of stations, mostly beyond the continental shelf. Interestingly, 30 specimens, ranging in length from 8.9 to 18.6 mm were captured 306 km off Coos Bay, Oreg., well beyond the continental shelf. Perhaps this wide ranging offshore occurrence of larvae and pelagic juveniles is related to their morphology. The larvae are quite stubby and deep bodied with particularly long head spines, features which could contribute to increased flotation and dispersal by currents. Most specimens were captured in oblique midwater trawl and bongo net tows. Three benthic juveniles were taken close to the coast in depths of 30 to 35 m.

Reported spawning times for *S. pinniger* are November to March off California (Phillips 1964) and January to March off Oregon, Washington, and British Columbia (Westrheim 1975). Larvae <10 mm were taken March through June, and larger pelagic specimens were taken March through August. The wide range in lengths, 9 to 25 mm in March, 7 to 38 mm in April, 8 to 34 mm in May, 9 to 43 mm in June, may be indicative of protracted and variable spawning. Benthic juveniles were taken in June and August.

Sebastes pinniger is one of the most abundant trawl-caught rockfish species on the continental shelf off Oregon together with *S. flavidus* and *S. entomelas* (Snytko and Fadeev 1974). In trawl surveys off Oregon it ranked either first or second only to *S. entomelas* in biomass over the shelf (Demory et al. 1976). It was one of the major contributors to "other rockfish" landings in Oregon during 1963-71 (Niska 1976). Larvae and juveniles were the most numerous in available collections of the three species described in this paper.

SEBASTES HELVOMACULATUS AYRES (Figures 12, 13)

Literature.—Westrheim et al. (see footnote 9) presented a schematic illustration of a preextrusion larva of *S. helvomaculatus* and described the pigment pattern in a tabular form. The latter table was also in Westrheim (1975). Preextrusion larvae (mean total length = 4.1 mm) have a ventral midline row of usually <16 (83% of 120 larvae) melanophores which stop short of the anus usually by as much as four myomeres. Pigment is absent from the dorsal midline, the head, nape, and lower jaw, and is usually not in the hypural region. The illustration shows some melanophores over the hindgut and ventrally beneath the yolk sac. Westrheim (1975) added that larvae of *S. helvomaculatus*, along with 10 other species which had been reared for several days, develop pigment spots on the head, nape, and/or lower jaw.

Identification (Table 10, Appendix Tables 2-6).—Twenty-six specimens of *S. helvomaculatus*, 7.7 to 183 mm long, were identified. Juveniles were identified using the following combination of characters obtained from specimens examined in this study:

Gill rakers = 28-31
Lateral line pores = 35-43
Pectoral fin rays = 15-17, usually 16
Anal fin soft rays = 5-6, usually 6
Dorsal fin soft rays = 12-14, usually 13
Supraocular spine = present
Interorbital space = concave.

Of the *Sebastes* species occurring off Oregon, *S. helvomaculatus* has the best fit to the above characters. *Sebastes aurora* and *S. elongatus* also agree with many of these characters, but *S. aurora* was eliminated since it has 24 to 28 gill rakers and *S. elongatus* was eliminated since it does not have a supraocular spine. Larval and juvenile specimens of *S. elongatus* identified from our collections are noticeably more slender than specimens of *S. helvomaculatus* and also are pigmented differently. Pigment pattern, body shape, time of occurrence, and constancy in number of anal fin soft rays and pectoral fin rays helped link together the developmental series.

Distinguishing Features.—Characters useful in distinguishing the smallest larva of *S. helvomaculatus* identified, 7.7 mm, are the pigmented fringes of the pectoral and pelvic fins; the general lack of body pigment; melanophores inside the tip of the lower jaw; narrow interorbital distance (31% HL); long, deeply serrated, parietal spines (27% HL); and relatively long pectoral fins

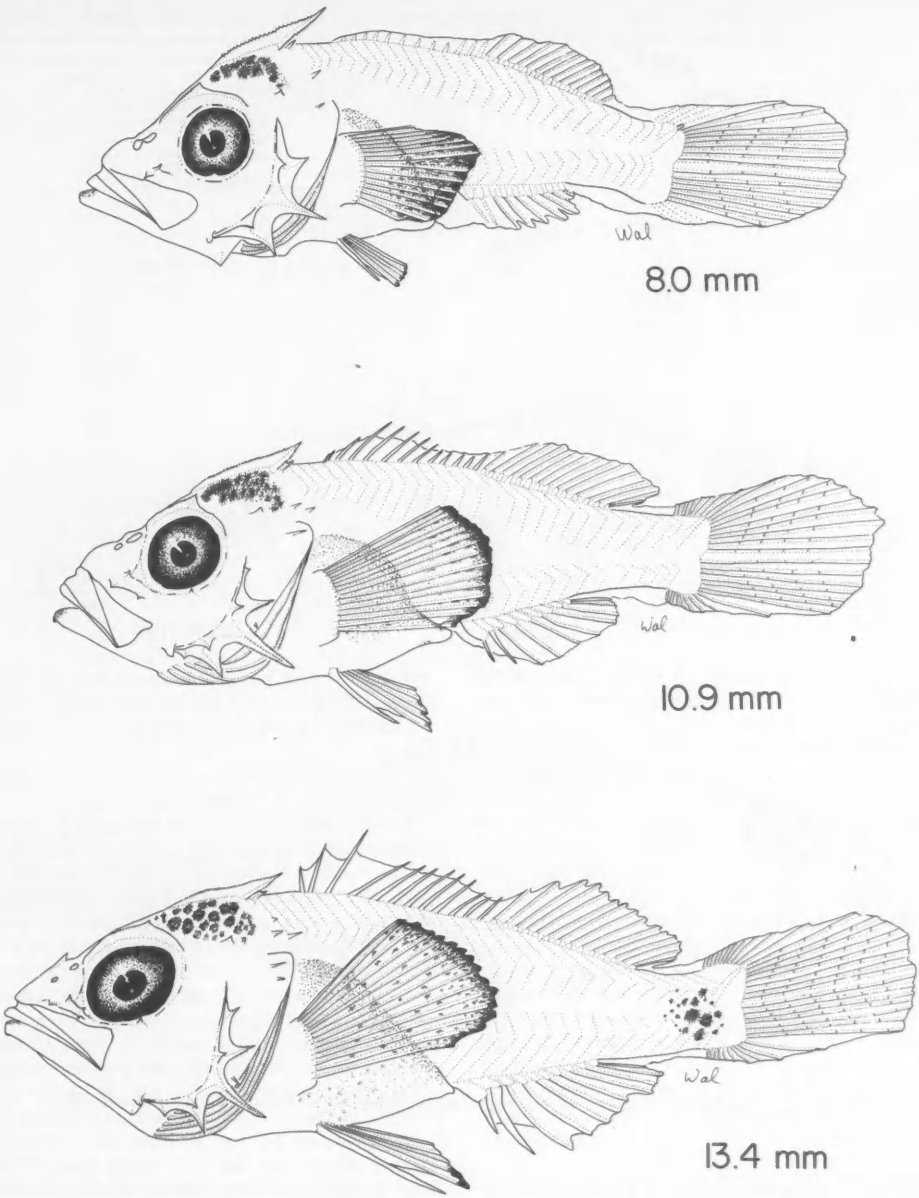

FIGURE 12.—Planktonic larvae (8.0, 10.9 mm) and transforming specimen (13.4 mm) of *Sebastes helvomaculatus*.

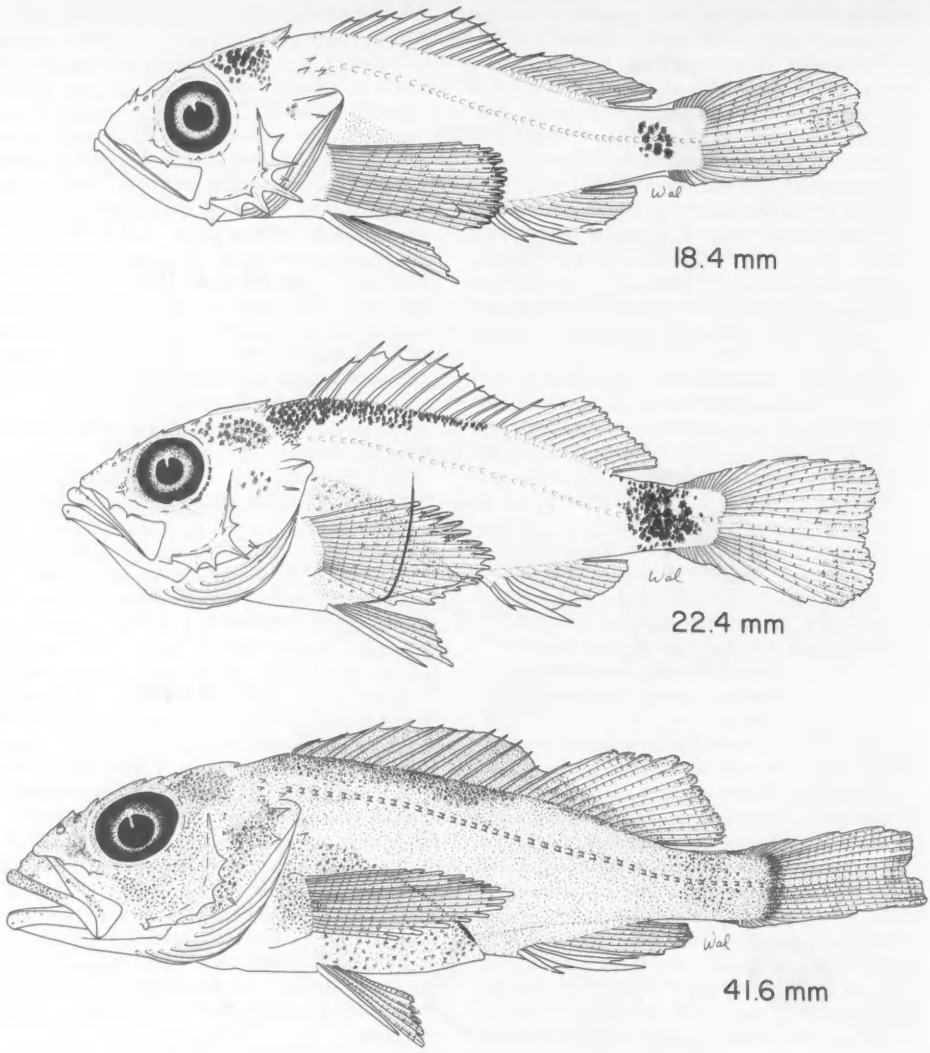

FIGURE 13.—Transforming specimen (18.4 mm) and pelagic juveniles (22.4, 41.6 mm) of *Sebastes helvomaculatus*.

(24% SL). Later stage larvae change very little in appearance from the smallest larva, except for an increase of dorsolateral internal gut pigment. A distinctive pigment patch appears on the caudal peduncle during the period of transformation from larva to pelagic juvenile. Meristics, presence of a supraocular spine, the concave shape and narrow width of the interorbital space, the patch of melanophores on the caudal peduncle, and the single melanistic pigment saddle extending pos-

TABLE 10.—Meristics from larvae and juveniles of *Sebastes helvomaculatus* off Oregon, based on unstained specimens. Specimens above dashed line are undergoing notochord flexion. All specimens had 8 superior and 7 inferior principal caudal fin rays and 7 branchiostegal rays on each side.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Pelvic fin spines and rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows
			Left	Right	Left	Right	Left	Right	Left	Right	
7.7	—	—	16	16	I,(1)	I,(1)	—	—	—	—	—
8.0	—	III[2],7	16	16	I,(1)	I,(1)	—	—	—	—	—
8.0	—	III[2],7	16	16	I,(1)	I,(1)	—	—	—	—	—
8.8	—	III[2],6	16	16	I,5	I,5	—	—	—	—	—
9.9	XIII[2],13	III[2],6	16	16	I,5	I,5	—	—	—	—	—
10.9	XIII[2],13	III[2],6	16	16	I,5	I,5	—	—	—	—	—
[3]12.0	XIII[2],13	III[2],6	16	16	I,5	I,5	—	—	—	—	—
[3]12.0	XIII[2],13	III[2],6	16	16	I,5	I,5	—	—	—	—	—
[3]13.4	XIII[2],13	III[2],7	16	16	I,5	I,5	—	—	—	—	—
[3]13.4	XIII[2],13	III[2],6	16	16	I,5	I,5	—	—	—	—	—
[3]13.6	XIII[2],13	III[2],6	16	16	I,5	I,5	—	21+9=30	—	—	—
[3]17.8	XIII[2],12	III[2],6	16	16	I,5	I,5	21+9=30	22+9=31	≈42	—	—
[3]17.9	XIII[2],12	III[2],6	16	16	I,5	I,5	21+9=30	21+9=30	—	—	—
[3]18.4	XIII[2],13	III[2],6	16	16	I,5	I,5	21+9=30	20+8=28	—	—	—
[3]18.4	XIII[2],12	III[2],6	16	16	I,5	I,5	21+9=30	21+9=30	42	—	—
[3]18.6	XIII[2],13	III,6	16	17	I,5	I,5	19+8=27	19+8=27	—	—	—
[4]19.8	XIII,13	III,6	16	16	I,5	I,5	21+8=29	21+8=29	≈40	—	—
[4]20.3	XIII,14	III,6	16	16	I,5	I,5	21+9=30	20+8=28	≈39	—	—
[4]21.6	XIII,13	III,6	16	16	I,5	I,5	21+8=29	21+8=29	≈39	—	—
[4]22.1	XIII,14	III,6	16	16	I,5	I,5	20+9=29	20+8=28	≈40	≈40	—
[4]22.2	XIII,13	III,6	16	16	I,5	I.5	20+8=28	20+8=28	≈38	≈38	—
[4]22.4	XIII,13	III,6	16	15	I,5	I,5	21+9=30	21+9=30	≈41	≈41	—
[4]23.8	XIII,12	III,5	16	16	I,5	I,5	20+9=29	20+9=29	≈43	≈43	—
[4]41.6	XIII,13	III,6	16	16	I,5	I,5	22+9=31	22+8=30	39	38	—
[5]136.4	XIII,13	III,6	16	15	I,5	I,3	21+9=30	21+9=30	35	35	—
[5]183	XIII,14	III,6	17	16	I,5	I,5	22+9=31	22+9=31	40	39	≈43

[1]Not formed.
[2]Posterior dorsal or anal spine appears as a soft ray.
[3]Transforming.
[4]Pelagic juvenile.
[5]Benthic juvenile.

teriorly from the nape to dorsal spine XI and ventrally about one-half the distance to the lateral line, all serve to distinguish pelagic juveniles.

General Development.—The smallest larva of *S. helvomaculatus* identified, 7.7 mm, is in the final stage of notochord flexion, which is completed by 8.8 mm. Transformation to pelagic juvenile begins in larvae ≈12 mm long with the initiation of spine formation in the dorsal and anal fin "prespines" and the appearance of a lateral pigment patch on the caudal peduncle. Transformation of the "prespines" to spines is completed in specimens >19 mm at which time some pigment appears beneath the spinous dorsal fin and pigment is added to the dorsal margin of the caudal peduncle pigment patch marking the beginning of pelagic juveniles pigmentation. More pigment is added beneath the first dorsal fin during the pelagic juvenile period although the saddle never becomes pronounced. Additional small external melanophores cover most of the fish by the end of the pelagic juvenile period, which probably lasts until ≈40-60 mm. The largest pelagic juvenile examined was 41.6 mm and the smallest benthic juvenile was 136.4 mm.

Morphology (Tables 4, 11).—Twenty-six specimens of *S. helvomaculatus*, 7.7 to 183 mm long, were measured for developmental morphology. Relative body depth/SL changes little at the pectoral fin base, decreasing slightly then increasing while it generally increases at the anus. Snout to anus distance increases from 56 to 63 or 64% SL and the snout to pelvic fin distance increases somewhat then decreases.

Head length increases slightly (41-42%) then decreases (38%) with respect to standard length. Eye diameter decreases (39-32% HL), as do the interorbital distance (31-15% HL) and snout length (32 or 33-27% HL). Upper jaw length increases from 44-46 to 52% HL. The length of the angle gill raker first increases (13-15% HL) then decreases (11%).

Larvae and juveniles <24 mm have a weak symphyseal knob which becomes less obvious with development.

Fin Development (Tables 4, 10, 11).—The adult complement of 15 to 18 (usually 16) pectoral fin rays can be counted on the smallest larva, 7.7 mm, of *S. helvomaculatus* although the ventralmost rays are not fully developed. Pectoral fins are

TABLE 11.—Measurements (millimeters) of larvae and juveniles of *Sebastes helvomaculatus* from waters off Oregon. Specimens above dashed line are undergoing notochord flexion.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at at pectoral fin base	Body depth at anus	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
7.7	9.5	4.3	3.2	1.1	1.5	1.2	1.0	2.5	1.6	1.9	0.96	0.64	1.0	3.0	1.0	0	1.0	—	[4]	[5]	[4]
8.0	9.8	4.4	3.2	0.96	1.5	1.3	1.0	2.8	1.7	2.0	1.0	0.68	1.2	3.3	0.90	0.04	0.90	—	[4]	[5]	[4]
8.0	9.9	4.6	3.4	1.1	1.4	1.3	1.0	2.6	1.6	1.7	1.0	0.66	1.0	3.3	0.78	0.08	0.78	—	[4]	[5]	[4]
8.8	10.9	5.2	3.9	1.3	1.4	1.4	1.2	2.9	1.9	2.2	1.1	0.40	1.3	3.6	0.78	0.10	1.2	0.48	[5]	0.80	[4]
9.9	12.3	5.8	4.1	1.3	1.6	1.5	1.3	3.3	2.6	2.4	1.1	1.2	1.6	4.0	0.80	0.22	1.3	0.56	0.88	1.2	0.60
10.9	13.4	6.5	4.4	1.5	1.8	1.6	1.4	3.7	2.8	2.6	1.2	1.6	1.7	4.5	0.70	0.22	—	0.62	0.82	1.3	0.76
[6]12.0	14.9	7.4	4.9	1.6	2.4	1.8	1.5	4.1	3.0	3.0	1.2	1.9	2.0	5.2	0.80	0.24	1.3	0.78	1.1	1.8	1.1
[6]12.0	14.4	7.1	4.9	1.5	2.6	1.9	1.5	4.3	3.1	3.4	1.3	2.1	2.4	5.2	0.72	0.24	—	0.88	—	1.9	1.2
[6]13.4	16.8	8.5	5.4	1.6	2.7	2.0	1.6	4.1	3.4	3.3	1.3	2.4	2.9	6.0	0.66	0.30	—	0.82	—	1.9	1.4
[6]13.4	16.8	8.5	5.6	1.8	2.6	2.0	1.6	4.7	3.6	3.6	1.5	2.4	2.6	5.7	0.72	0.26	1.3	0.72	—	1.9	1.3
[6]13.6	16.8	8.5	5.8	2.2	2.4	2.0	1.5	4.4	3.3	3.3	1.3	2.2	2.4	6.2	—	0.28	1.1	0.80	1.4	1.9	1.4
[6]17.8	22.1	10.7	7.5	2.7	3.2	2.4	1.8	5.7	4.5	4.5	1.6	3.4	3.8	7.2	1.0	0.32	—	1.1	2.3	2.6	2.3
[6]17.9	22.2	11.2	7.3	2.6	2.9	2.4	1.7	5.7	4.2	4.5	1.7	3.1	3.2	8.0	0.80	0.28	1.3	1.1	—	2.8	2.2
[6]18.4	22.9	11.0	6.7	2.1	3.0	2.5	1.9	5.9	4.3	4.9	1.8	3.2	3.7	7.0	0.96	0.36	1.4	1.1	2.1	—	1.9
[6]18.4	23.0	11.0	7.2	1.8	3.4	2.7	1.8	5.7	4.4	5.2	1.8	3.4	3.7	7.0	0.70	0.34	1.3	1.1	2.7	3.0	2.6
[6]18.6	21.1	12.0	8.0	2.7	3.4	2.6	1.9	5.8	4.3	4.8	1.8	3.4	3.4	8.8	0.72	0.24	1.3	1.1	—	2.6	—
[7]19.8	24.6	12.0	8.2	2.8	3.3	2.8	2.1	6.4	4.6	5.2	1.8	3.1	3.6	8.2	—	0.36	1.3	1.2	—	2.6	2.2
[7]20.3	25.3	12.8	8.4	2.8	4.0	2.8	2.0	6.2	4.7	5.3	1.8	—	4.1	9.0	0.80	0.34	1.3	1.2	—	3.0	2.0
[7]21.6	26.4	13.0	8.4	2.5	4.0	2.8	2.0	7.1	5.2	5.7	2.0	—	4.0	8.6	—	0.14	—	1.2	—	3.2	3.0
[7]22.1	26.4	14.2	8.9	3.0	4.2	3.0	1.9	7.2	5.3	5.9	2.0	3.4	4.4	9.8	0.72	0.26	—	1.4	2.8	3.2	2.7
[7]22.2	27.7	14.6	9.3	3.0	4.2	3.0	1.9	6.7	5.1	5.9	2.0	4.2	4.4	10.7	0.46	0.32	—	1.3	2.6	3.1	3.1
[7]22.4	27.7	13.4	8.4	2.6	3.8	3.1	2.0	7.2	5.6	6.0	2.0	4.1	4.8	8.8	—	0.44	1.1	1.3	3.0	3.2	3.2
[7]23.8	29.1	15.7	9.4	3.1	4.3	2.9	1.9	7.2	5.2	6.4	2.2	3.9	4.3	10.7	0.40	0.30	—	1.2	2.8	3.4	—
[7]41.6	49.8	26.2	16.5	4.4	7.0	5.7	2.2	11.8	8.8	7.0	3.4	5.6	7.2	16.6	0.18	—	0.42	2.1	4.9	6.1	6.4
[8]136.4	169	86.0	51.8	14.0	26.7	18.3	6.7	44.0	32.3	37.6	12.0	19.7	30.0	53.8	1.6	—	1.3	5.7	17.4	20.7	27.0
[8]183	219	118.1	68.1	18.0	35.8	18.9	11.2	63.3	49.4	48.4	18.0	28.2	42.9	74.5	—	—	0.32	7.0	27.6	31.0	31.0

[1]Usually third or fourth in larvae, fifth or sixth in juveniles.
[2]Usually midfin.
[3]The second spine.
[4]Not formed.
[5]Forming.
[6]Transforming.
[7]Pelagic juvenile.
[8]Benthic juvenile.

rather long, averaging 24-26% SL during the pelagic period. Depth of the pectoral fin decreases from 12% in flexion larvae to 9% in benthic juveniles.

Pelvic fin spines and developing rays are visible on the 7.7 mm larva. The adult complement of I, 5 is countable on the smallest postflexion larva, 8.8 mm. The relative length of the pelvic fin increases from 14 to 23% SL with development. The pelvic spine, always shorter than the pelvic fin rays, increases from 8% SL in flexion larvae to 18% in transforming larvae and then decreases to 15% in benthic juveniles.

The adult complement of 8 + 7 principal caudal fin rays can be counted on the 7.7 mm preflexion larva. Flexion is completed by 8.8 mm. Superior and inferior secondary caudal rays on two stained juveniles 22.4 and 23.8 mm long, were 12 + 12 and 11 + 11, respectively.

Bases of dorsal and anal fin spines and rays are visible on the 7.7 mm larva. Rays and spines (including "prespines") are fully formed by 9.9 mm and the adult complements can be counted. "Prespines" become spines in specimens >19 mm. The longest dorsal spine increases from 19% HL in postflexion larvae to 37% in benthic juveniles. The longest dorsal ray, always longer than the longest dorsal spine, increases from 23 to 43% HL during development. The longest anal spine increases from 16 to 49% HL.

Spination (Tables 4, 12).—Spines on the left side of the head of the smallest *S. helvomaculatus* (7.7 mm) include the parietal; first and third anterior preopercular spines; second, third, and fourth posterior preopercular spines; postocular; pterotic; inferior posttemporal; and first spine of the superior infraorbital series.

The parietal spine and ridge are deeply serrated in larvae and pelagic juveniles, but the serrations are no longer visible by 41.6 mm. The parietal spine is very long in flexion larvae, averaging 27% HL. Its length decreases with development to 3% HL in benthic juveniles. The much smaller nuchal spine, which appears by 8 mm, averages 2% HL in flexion larvae and increases to 4 or 5% in postflex-

TABLE 12.—Development of spines in the head region of *Sebastes helvomaculatus* larvae and juveniles. Specimens above dashed line are undergoing notochord flexion. + denotes spine present and – denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series) 1st	2d	3d	Preopercular (posterior series) 1st	2d	3d	4th	5th	Opercular Superior	Inferior	Interopercular	Subopercular	Preocular	Supraocular	Postocular
7.7	+	–	+	–	+	–	+	+	+	–	–	–	–	–	–	–	+
8.0	+	–	+	–	+	–	+	+	+	–	–	–	–	–	–	–	+
8.0	+	+	+	–	+	–	+	+	+	–	–	–	–	–	–	–	+
8.8	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
9.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
10.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]12.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]12.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]13.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[1]13.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	([2])	([2])	+
[1]13.6	+	+	+	–	+	+	+	+	+	+	+	+	+	–	([2])	([2])	+
[1]17.8	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]17.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]18.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]18.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[1]18.6	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[3]19.8	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[3]20.3	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[3]21.6	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[3]22.1	+	+	+	–	+	+	+	+	+	+	+	+	+	–	+	+	+
[3]22.2	+	+	([2])	–	([2])	+	+	+	+	+	+	+	+	–	+	+	+
[3]22.4	+	+	([2])	–	([2])	+	+	+	+	+	+	+	+	–	+	+	+
[3]23.8	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[3]41.6	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[4]136.4	+	+	–	–	–	+	+	+	+	+	+	+	+	–	+	+	+
[4]183	+	+	–	–	–	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 12.—Continued.

Standard length (mm)	Infraorbitals Inferior 1st	2d	3d	Superior 1st	2d	3d	4th	Nasal	Coronal	Tympanic	Pterotic	Posttemporal Superior	Inferior	Supracleithral	Cleithral
7.7	–	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.0	–	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.0	–	–	–	+	–	–	–	–	–	–	+	–	+	–	–
8.8	+	+	–	+	–	–	+	–	–	–	+	–	+	+	–
9.9	+	+	–	+	–	–	+	([2])	–	–	+	–	+	+	–
10.9	+	+	–	+	–	–	+	([2])	–	–	+	–	+	+	–
[1]12.0	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
[1]12.0	+	+	–	+	+	–	+	+	–	–	+	–	+	+	–
[1]13.4	+	+	–	+	+	–	+	+	–	–	+	+	+	+	–
[1]13.4	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]13.6	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]17.8	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]17.9	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]18.4	+	+	–	+	+	+	+	+	–	–	+	+	+	+	([2])
[1]18.4	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[1]18.6	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[3]19.8	+	+	–	+	+	+	+	+	–	–	+	+	+	+	–
[3]20.3	+	+	–	+	+	+	+	+	–	–	([2])	+	+	+	([2])
[3]21.6	+	+	–	+	+	+	+	+	–	–	([2])	+	+	+	([2])
[3]22.1	+	+	–	+	+	+	+	+	–	–	([2])	+	+	+	([2])
[3]22.2	+	+	–	+	([2])	+	+	+	–	–	([2])	+	+	+	–
[3]22.4	+	+	–	+	([2])	([2])	([2])	+	–	–	([2])	+	+	+	+
[3]23.8	+	+	–	–	–	–	–	+	–	–	([2])	+	+	+	+
[3]41.6	+	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]136.4	+	+	–	–	–	–	–	+	–	+	–	+	+	+	+
[4]183	+	+	–	–	–	–	–	+	–	+	–	+	+	+	–

[1]Transforming.
[2]Bump indicating beginning of spine formation.
[3]Pelagic juvenile.
[4]Benthic juvenile.

ion, transforming, and pelagic juvenile stages. The nuchal and parietal spines are fused together by the time juveniles are 42 mm long.

The posterior preopercular spine series is prominent in *S. helvomaculatus* larvae. The third spine of the series is weakly serrated in larvae >8 mm up to pelagic juveniles. It is relatively long in larvae averaging 27 to 31% HL in flexion and postflexion stages. Its length decreases to 2% in benthic juveniles when it is no longer serrated.

Very weak serrations appear on the second and fourth posterior preopercular spines of most larger larvae and smaller pelagic juveniles. All five posterior preopercular spines are present on specimens >8.0 mm. The first and third anterior preopercular spines seen on the smallest larva are no longer visible on specimens >23 mm. The second anterior preopercular spine never develops.

The superior and inferior opercular spines are present on all specimens >8 mm. The interopercular spine is present at 8.8 mm and persists into benthic juveniles. The subopercular spine is present just above the interopercular spine on the largest benthic juvenile, 183 mm.

The supraocular ridge and the anterior margin of the postocular spine are serrated on specimens up to 23.8 mm. The preocular and supraocular spines are first seen as bumps in a 13.4 mm specimen. Serrations are present on the supraocular spine but disappear along with those on the supraocular ridge on larger pelagic juveniles.

The first superior infraorbital spine is visible up to 23 mm. The second superior infraorbital spine appears on specimens 12 to 23 mm. The fourth superior infraorbital spine is present on larvae >8 mm and the third superior infraorbital spine is present on larvae >13.4 mm. The third and fourth spines both disappear by 23 mm. The first and second spines of the inferior infraorbital series are present on all specimens >8 mm but appear only as blunt projections on benthic juveniles. The third inferior infraorbital spine never develops. The nasal spine appears as a bump by 9 mm and becomes strong and sharp during the larval period.

The tympanic spine develops by 41.6 mm and appears as a strong sharp spine on benthic juveniles. The pterotic spine is present on all specimens >41.6 mm. The inferior posttemporal spine is present on all specimens examined but is minute on the two benthic juveniles, 136 and 183 mm, and probably disappears in larger specimens. The supracleithral spine is present on all specimens >8.0 mm. The superior posttemporal appears at 13.4 mm and is present on all larger specimens. Posterior to the opercle the cleithral spine appears on all specimens >19 mm.

Scale Formation.—Lateral line pores first appear anteriorly and are visible on specimens >17 mm. Scale formation begins on pelagic juveniles >23 mm.

Pigmentation.—The smallest larva of *S. helvomaculatus*, 7.7 mm (similar to the 8.0 mm specimen illustrated), has pigment on the head over the brain. Melanophores line the inner tip of the lower jaw. In the abdominal region, an internal melanistic shield is present over the dorsolateral surface of the gut. No other pigment is visible on the body. The pectoral and pelvic fins are fringed with expanded and fused melanophores and have a light scattering of more contracted, elongate melanophores on the fin blades. Both inner and outer pectoral fin base surfaces are unpigmented.

During larval development, pigment over the brain becomes obscured. At 13.4 mm pigment inside the lower jaw disappears. Specimens >17 mm develop two to six internal melanophores dorsally on the opercle.

During the transformation period, 12.0 to 18.6 mm, two or three melanophores may appear just posterior to the orbit on specimens >18 mm. Internal gut pigment increases ventrolaterally reaching the ventral surface of the gut by 17.9 mm. The anterior margin of the cleithrum is usually unpigmented. A patch of 9 to 10 large stellate melanophores appears laterally on the caudal peduncle at 12.0 mm at the beginning of the transformation period. Melanophores are added to this patch until it extends to the dorsal body surface at ≈18 mm. Melanophores in this patch often appear expanded and fused. The pectoral and pelvic fins remain fringed with pigment although this may not be obvious if the fins are frayed. The number of melanophores on the fin blades generally decreases.

During the pelagic juvenile period, 19.8 to 41.6 mm, pigment appears over the head surface, snout, and upper lip of specimens >22 mm. Melanophores are added along the posteroventral margin of the orbit and a patch of melanophores appears just dorsal to the first superior infraorbital spine. The internal pigment patch on the operculum remains distinguishable. Internal gut pigment becomes increasingly obscured by musculature. A single saddle of melanophores develops on the dorsal surface of the body over the nape and beneath the spinous dorsal fin anterior to dorsal spine XI. The first melanophores generally appear there at the onset of the pelagic juvenile stage, although a few may develop earlier. This saddle extends ventrolaterally from the nape to the vicinity of the supracleithral spine and from the spinous dorsal fin halfway to the lateral line by 22

mm. By 41.6 mm small external melanophores cover all but the ventralmost one-fourth of the abdominal region including most of the pectoral fin base and the dorsal one-fourth of the gut region. The dorsal saddle and internal gut pigmentation still appear as more darkly pigmented areas. The caudal peduncle patch expands to the dorsal and ventral body margins. Specimens >20 mm have a few melanophores extending anteriorly from the peduncle patch along the dorsal body margin under the posteriormost dorsal rays. By 41.6 mm the entire tail region of the body is also covered with small external melanophores, although the caudal peduncle patch and dorsal midline melanophores remain visible. Pectoral and pelvic fins lose all pigment by 41.6 mm, except for a patch of small melanophores on the base of the central pectoral rays. The spinous dorsal fin becomes completely covered with small melanophores by 41.6 mm and small melanophores cover the proximal one-fourth of the soft dorsal fin. Small melanophores extend onto the bases of the caudal fin rays by 41.6 mm.

Melanistic pigment is inconspicuous on the benthic juveniles examined, 136 and 183 mm. The caudal peduncle pigment patch is no longer visible.

Occurrence (Figures 14, 15).—*Sebastes helvomaculatus* ranges from Coronado Bank, off San Diego, Calif., to Albatross Bank, Gulf of Alaska, and occurs in depths from 133 to 456 m (Chen 1971). It is apparently primarily a deepwater species judging by some of the older common names given to it, "deep-water scacciatale" and "deep-water scratch-tail" (Phillips 1957). The largest numbers and smallest larvae were taken 83 and 120 km off Newport beyond the continental shelf break. Most pelagic juveniles were taken at the same locations as the larvae, probably reflecting the increased sampling effort in that area. One benthic juvenile, 136 mm, was taken in an otter trawl at a depth of 370 m (lat. 44°47.9′ N, long. 124°40.9′ W). A second juvenile, 183 mm, was collected after a seismic profiling explosion on Stonewall Bank (≈lat. 44°30′ N, long. 124°25′ W).

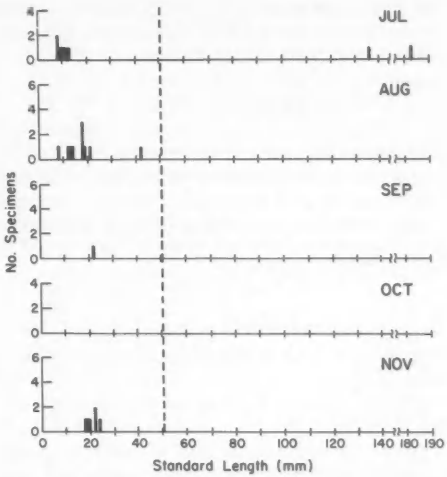

FIGURE 15.—Seasonal occurrence of larvae and juveniles of *Sebastes helvomaculatus* off Oregon. Data from 1961 to 1976 combined. Dashed line separates pelagic and benthic stages.

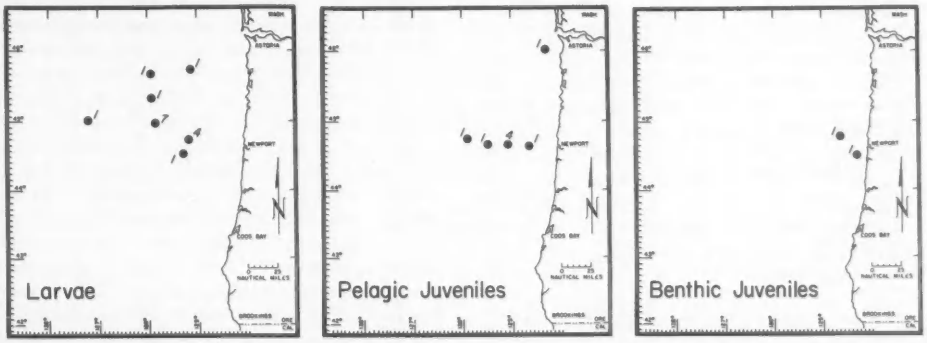

FIGURE 14.—Number of specimens and location of capture of larvae and juveniles of *Sebastes helvomaculatus* off Oregon (1961-76) described in this paper.

Based on examination of gonads, Westrheim (1975) reported that parturition of *S. helvomaculatus* takes place primarily in June from Oregon to British Columbia. We took small larvae >10 mm only in July and August. Pelagic juveniles were captured in August, September, and November. The two benthic juveniles were taken in July.

Adults of *S. helvomaculatus* are uncommon in Oregon trawl landings (Niska 1976). They ranked 9th and 16th in biomass in trawl surveys on the Oregon continental shelf and 8th on the continental slope together with *S. elongatus* and *S. zacentrus* (Demory et al. 1976). Larvae and juveniles were not common in our collections.

COMPARISONS (TABLE 13)

Prior to this paper, developmental series of 7 of the 69 northeast Pacific (including the Gulf of California) species of *Sebastes* had been described: *S. cortezi*, *S.* sp. Gulf Type A, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, and *S. paucispinis* (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978). While pelagic stages of these species exhibit some similarities to the three described by us, they also differ in a number of characters. The most notable of these are discussed here in a comparative sense.

Flexion and postlarvae of *S. pinniger* are quite deep bodied (38-40% SL) although body depth at the pectoral fin base decreases considerably (33% SL) by the pelagic juvenile stage. Larvae and juveniles of *S. melanostomus* are also deep bodied. Pelagic stages of *S. jordani* are comparatively slender (17-24% SL). Prior to completion of notochord flexion, *S. paucispinis* is also relatively slender bodied. Pelagic stages of *S. crameri*, *S. helvomaculatus*, *S. levis*, and *S. macdonaldi* are somewhat intermediate in body depth. Snout to

TABLE 13.—Morphometric comparison of larvae and juveniles of nine species of *Sebastes* from the northeast Pacific. Values are mean percentages of body proportions related to standard length (SL) or head length (HL). Numbers in italics represent values for two developmental stages combined.

Item	*S. cortezi*[1]	*S. crameri*	*S.* Gulf Type A[1]	*S. helvomaculatus*	*S. jordani*[1]	*S. levis*[1]	*S. macdonaldi*[1]	*S. melanostomus*[1]	*S. paucispinis*[1]	*S. pinniger*
Body depth at pectoral fin base/SL:										
Preflexion	—	—	—	—	17	—	23	—	20	—
Flexion	—	32	—	33	21	28	32	36	23	40
Postflexion	—	32	—	33	*24*	*34*	*34*	*39*	*30*	38
Transforming	—	32	—	33						36
Pelagic juvenile	—	33	—	31	22	35	31	37	27	33
Benthic juvenile	—	34	—	33	—	—	—	—	—	35
Snout to anus length/SL:										
Preflexion	—	—	—	—	36	—	42	—	41	—
Flexion	—	54	—	56	42	49	52	57	45	59
Postflexion	—	60	—	59	*51*	*59*	*60*	*59*	*57*	60
Transforming	—	61	—	62						61
Pelagic juvenile	—	62	—	63	53	63	64	64	62	61
Benthic juvenile	—	65	—	64	—	—	—	—	—	64
Pectoral fin length/SL:										
Preflexion	7-9	—	6-9	—	7	9	8	—	—	—
Flexion	9-12	17	—	24	8	35	13	20	27	25
Postflexion	*21*	21	20	24	11	*45*	*19*	*22*	*36*	25
Transforming		27	—	26	20					27
Pelagic juvenile	23	32	—	27	22	41	30	26	28	26
Benthic juvenile	—	30	—	27	—	—	—	—	—	24
Pelvic fin length/SL:										
Preflexion	—	—	—	—	—	—	4	—	—	—
Flexion	—	7	—	14	1	6	6	12	14	14
Postflexion	—	15	—	16	*9*	*21*	*14*	*16*	*35*	17
Transforming	—	21	—	19						23
Pelagic juvenile	—	21	—	19	14	24	22	20	25	22
Benthic juvenile	—	21	—	23	—	—	—	—	—	21
Parietal spine length/HL:										
Preflexion	—	—	—	—	—	—	—	—	—	—
Flexion	*21-22*	6	*25-34*	27	—	—	*20-23*	—	—	24
Postflexion		7		18	—	—		—	—	20
Transforming	—	6	—	13	—	—	—	—	—	10
Pelagic juvenile	—	3	—		—	—	—	—	—	7
Benthic juvenile	—	—	—		—	—	—	—	—	—
Preopercular spine length/HL:										
Preflexion	—	—	—	—	—	—	—	—	—	—
Flexion	—	18	—	27	—	—	*35*	—	—	34
Postflexion	—	17	—	31	—	—		—	—	32
Transforming	—	18	—	20	—	—	—	—	—	24
Pelagic juvenile	—	12	—	12	—	—	—	—	—	13
Benthic juvenile	—	7	—	2	—	—	—	—	—	5

[1]Values from Moser et al. (1977) and Moser and Ahlstrom (1978).

anus distance is markedly shorter in larvae and juveniles of *S. jordani* (36-53% SL) compared with the other species.

The pectoral fins in *S. jordani* remain comparatively short (7-22% SL) during pelagic development while those of *S. levis* attain an exceptional size (to 45% SL). Late larval stages of *S. paucispinis* also have outstandingly long pectoral fins (36% SL). Fin lengths among the other species are intermediate by comparison and vary to a lesser degree during development. The pelvic fins of *S. paucispinis* also become extraordinarily long (35% SL) during the late larval period whereas those of *S. jordani* remain relatively short.

Parietal spine length varies among species with the largest spines appearing in early larvae of *S. helvomaculatus* (27% HL) and *S.* sp. Gulf Type A (25-34% HL). This spine is noticeablely short on *S. crameri* (3-7% HL) during the entire pelagic phase. The third preopercular spine is outstandingly long on early larvae of *S. macdonaldi* (35% HL) and *S. pinniger* (34% HL) but is comparatively short on *S. crameri* (17% HL) as is the parietal.

Pigmentation on the paired fins varies from the unpigmented condition in *S. jordani* to the heavily pigmented fins of *S. macdonaldi* and *S. crameri*. The pectoral fins of *S. cortezi* are pigmented at the fin base but not the outer margin, while pigment is primarily concentrated on the outer margin of the fins in *S. paucispinis*, *S. levis*, and *S. helvomaculatus* at least during the early pelagic period. Pectoral fins of *S. pinniger*, *S. melanostomus*, and *S.* sp. Gulf Type A are lightly pigmented.

General body pigmentation differs among the species considered. Larvae of *S. pinniger* have a characteristic lack of body pigment. A patch of nape pigment develops early in *S. crameri* and *S. macdonaldi*, appearing more pronounced in the former species. Postflexion larvae of both *S. crameri* and *S. macdonaldi* develop pigment on the entire spinous dorsal fin. A characteristic black blotch develops on the posterior portion of the first dorsal fin in pelagic juveniles of *S. pinniger*. Larvae of *S. melanostomus*, *S. paucispinis*, and *S. macdonaldi* have a characteristically low number of ventral midline melanophores, 4 to 11 (mean 8), 6 to 14 (mean 9), and 6 to 14 (mean 8), respectively. A patch of pigment forms on the caudal peduncle of *S. helvomaculatus*, *S. paucispinis*, *S. jordani*, and *S. cortezi*. The form of the patch varies with the species and is most pronounced in *S. helvomaculatus*. One characteristic melanophore appears at the base of the caudal fin in *S. cortezi*, while melanophores form a line of pigment at the base of the caudal fin in *S. jordani*, but not in any of the other species.

Pelagic juveniles of *S. helvomaculatus* develop only one melanistic pigment saddle beneath the spinous dorsal fin. Five distinct saddles form on *S. macdonaldi*, *S. crameri*, *S. levis*, *S. paucispinis*, and *S. pinniger* in comparable locations on the body although a more blotchy pattern develops on *S. pinniger*. On *S. melanostomus*, three pronounced melanistic bars develop on the body. Apparently no obvious saddles or bars develop on pelagic juveniles of *S. jordani* or *S. cortezi*.

These comparisons together with distinguishing features of each species given by us, Moser (1972), Moser et al. (1977), and Moser and Ahlstrom (1978), and range of occurrence should aid in identification of all but the smallest larvae. As additional species are described, such comparisons may also provide insight into relationships within the genus *Sebastes*.

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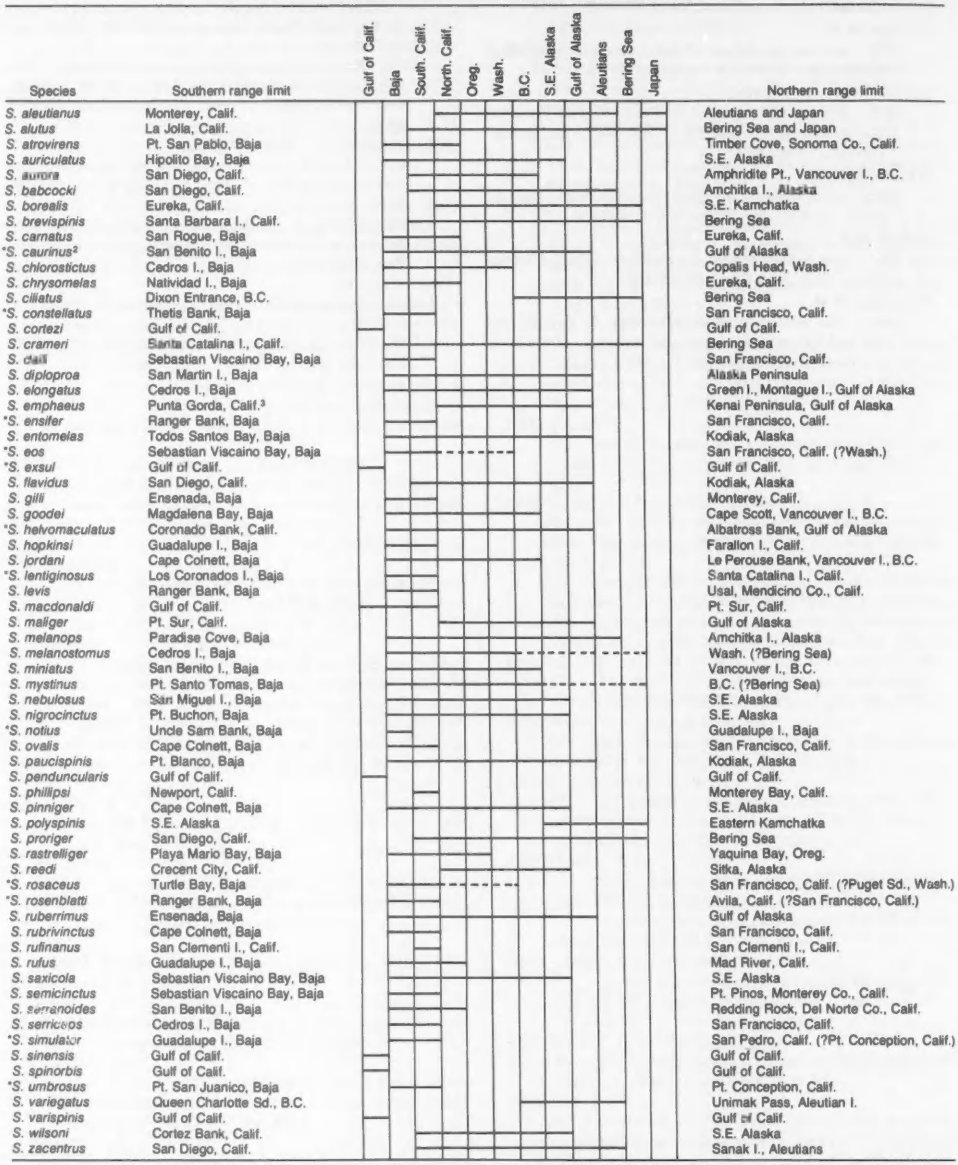
APPENDIX TABLE 1.—Ranges of eastern North Pacific species of *Sebastes*.[1] This list does not include one new species being described by Lea and Fitch (Chen 1975). Asterisk indicates species in the subgenus *Sebastomus*.



Species	Southern range limit	Northern range limit
S. aleutianus	Monterey, Calif.	Aleutians and Japan
S. alutus	La Jolla, Calif.	Bering Sea and Japan
S. atrovirens	Pt. San Pablo, Baja	Timber Cove, Sonoma Co., Calif.
S. auriculatus	Hipolito Bay, Baja	S.E. Alaska
S. aurora	San Diego, Calif.	Amphridite Pt., Vancouver I., B.C.
S. babcocki	San Diego, Calif.	Amchitka I., Alaska
S. borealis	Eureka, Calif.	S.E. Kamchatka
S. brevispinis	Santa Barbara I., Calif.	Bering Sea
S. carnatus	San Rogue, Baja	Eureka, Calif.
**S. caurinus*[2]	San Benito I., Baja	Gulf of Alaska
S. chlorostictus	Cedros I., Baja	Copalis Head, Wash.
S. chrysomelas	Natividad I., Baja	Eureka, Calif.
S. ciliatus	Dixon Entrance, B.C.	Bering Sea
**S. constellatus*	Thetis Bank, Baja	San Francisco, Calif.
S. cortezi	Gulf of Calif.	Gulf of Calif.
S. crameri	Santa Catalina I., Calif.	Bering Sea
S. dalli	Sebastian Viscaino Bay, Baja	San Francisco, Calif.
S. diploproa	San Martin I., Baja	Alaska Peninsula
S. elongatus	Cedros I., Baja	Green I., Montague I., Gulf of Alaska
S. emphaeus	Punta Gorda, Calif.[3]	Kenai Peninsula, Gulf of Alaska
**S. ensifer*	Ranger Bank, Baja	San Francisco, Calif.
S. entomelas	Todos Santos Bay, Baja	Kodiak, Alaska
**S. eos*	Sebastian Viscaino Bay, Baja	San Francisco, Calif. (?Wash.)
**S. exsul*	Gulf of Calif.	Gulf of Calif.
S. flavidus	San Diego, Calif.	Kodiak, Alaska
S. gilli	Ensenada, Baja	Monterey, Calif.
S. goodei	Magdalena Bay, Baja	Cape Scott, Vancouver I., B.C.
**S. helvomaculatus*	Coronado Bank, Calif.	Albatross Bank, Gulf of Alaska
S. hopkinsi	Guadalupe I., Baja	Farallon I., Calif.
S. jordani	Cape Colnett, Baja	Le Perouse Bank, Vancouver I., B.C.
**S. lentiginosus*	Los Coronados I., Baja	Santa Catalina I., Calif.
S. levis	Ranger Bank, Baja	Usal, Mendicino Co., Calif.
S. macdonaldi	Gulf of Calif.	Pt. Sur, Calif.
S. maliger	Pt. Sur, Calif.	Gulf of Alaska
S. melanops	Paradise Cove, Baja	Amchitka I., Alaska
S. melanostomus	Cedros I., Baja	Wash. (?Bering Sea)
S. miniatus	San Benito I., Baja	Vancouver I., B.C.
S. mystinus	Pt. Santo Tomas, Baja	B.C. (?Bering Sea)
S. nebulosus	San Miguel I., Baja	S.E. Alaska
S. nigrocinctus	Pt. Buchon, Baja	S.E. Alaska
**S. notius*	Uncle Sam Bank, Baja	Guadalupe I., Baja
S. ovalis	Cape Colnett, Baja	San Francisco, Calif.
S. paucispinis	Pt. Blanco, Baja	Kodiak, Alaska
S. penduncularis	Gulf of Calif.	Gulf of Calif.
S. phillipsi	Newport, Calif.	Monterey Bay, Calif.
S. pinniger	Cape Colnett, Baja	S.E. Alaska
S. polyspinis	S.E. Alaska	Eastern Kamchatka
S. proriger	San Diego, Calif.	Bering Sea
S. rastrelliger	Playa Mario Bay, Baja	Yaquina Bay, Oreg.
S. reedi	Crecent City, Calif.	Sitka, Alaska
**S. rosaceus*	Turtle Bay, Baja	San Francisco, Calif. (?Puget Sd., Wash.)
**S. rosenblatti*	Ranger Bank, Baja	Avila, Calif. (?San Francisco, Calif.)
S. ruberrimus	Ensenada, Baja	Gulf of Alaska
S. rubrivinctus	Cape Colnett, Baja	San Francisco, Calif.
S. rufinanus	San Clementi I., Calif.	San Clementi I., Calif.
S. rufus	Guadalupe I., Baja	Mad River, Calif.
S. saxicola	Sebastian Viscaino Bay, Baja	S.E. Alaska
S. semicinctus	Sebastian Viscaino Bay, Baja	Pt. Pinos, Monterey Co., Calif.
S. serranoides	San Benito I., Baja	Redding Rock, Del Norte Co., Calif.
S. serriceps	Cedros I., Baja	San Francisco, Calif.
**S. simulator*	Guadalupe I., Baja	San Pedro, Calif. (?Pt. Conception, Calif.)
S. sinensis	Gulf of Calif.	Gulf of Calif.
S. spinorbis	Gulf of Calif.	Gulf of Calif.
**S. umbrosus*	Pt. San Juanico, Baja	Pt. Conception, Calif.
S. variegatus	Queen Charlotte Sd., B.C.	Unimak Pass, Aleutian I.
S. varispinis	Gulf of Calif.	Gulf of Calif.
S. wilsoni	Cortez Bank, Calif.	S.E. Alaska
S. zacentrus	San Diego, Calif.	Sanak I., Aleutians

[1]Compiled from Bailey et al. (1970), Chen (1971), Lea and Fitch (1972), Miller and Lea (1972), Quast and Hall (1972), Rosenblatt and Chen (1972), Barsukov (1973), Hart (1973), and Chen (1975), and original data for *S. emphaeus*. No records from the Sea of Okhotsk.

[2]Includes *S. vexillaris* (Chen 1975; W. N. Eschmeyer, Senior Curator for Research, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, pers. commun. November 1976).

[3]Based on data obtained during this study.

APPENDIX TABLE 2.—Chart showing interorbital curvature and presence or absence of the supraocular spine for rockfishes (*Sebastes* spp.) occurring off Oregon.[1] x indicates usual condition; o indicates occasional occurrence.

	Interorbital					Interorbital			
	Flat-convex		Concave			Flat-convex		Concave	
	Supraocular spine		Supraocular spine			Supraocular spine		Supraocular spine	
Species	Present	Absent	Present	Absent	Species	Present	Absent	Present	Absent
S. aleutianus	x				*S. jordani*		x		
S. alutus	x	o			*S. maliger*	o	x	o	x
S. auriculatus		x			*S. melanops*		x		
S. aurora	x		x		*S. melanostomus*	x		x	
S. babcocki				x	*S. miniatus*	x			
S. borealis	x		x		*S. mystinus*		x		
S. brevispinis	o	x			*S. nebulosus*				x
S. caurinus		x		x	*S. nigrocinctus*			o	x
S. chlorostictus			x		*S. paucispinis*		x		
S. crameri	x				*S. pinniger*	x			
S. diploproa		x		x	*S. proriger*		x		
S. elongatus				x	*S. rastrelliger*		x		
S. emphaeus		x			*S. reedi*	x	o		
S. entomelas	o	x			*S. rosaceus*[2]			x	
S. eos[2]			x		*S. ruberrimus*			x	
S. flavidus		x			*S. saxicola*		x		x
S. goodei		x			*S. wilsoni*	o	x	o	x
S. helvomaculatus			x		*S. zacentrus*	o	x	o	x

[1]Compiled from Phillips (1957), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 3.—Numbers of dorsal, anal, and pectoral fin soft rays for rockfishes (*Sebastes* spp.) occurring off Oregon.[1] x indicates usual numbers, o indicates occasional occurence.

	Dorsal fin rays							Anal fin rays						Pectoral fin rays							
Species	11	12	13	14	15	16	17	5	6	7	8	9	10	11	15	16	17	18	19	20	21	22
S. aleutianus		o	x	x	o				o	x	o						o	x	x			
S. alutus			o	x	x	x	x		o	o	x	x			o	o	o	x	o			
S. auriculatus		o	x	o	o			o	o	x	o				o	o	o	x	o			
S. aurora		o	x	o				o	x							o	o	o				
S. babcocki			o	x	o				x	x								o	o	x	o		
S. borealis		o	x	o	o				o	x	o							o	o	o	o		
S. brevispinis				o	o	o	o			x	o					o	o	o				
S. caurinus	o	o	x	o				o	x	o						o	x	o				
S. chlorostictus	o	x	o	o	o			o	x	o						o	x	o				
S. crameri		o	x	x				o	o	x								o	x	o		
S. diploproa	o	x	x	o					x	x	o						o	x	o			
S. elongatus		o	x	o					x	o						x	x	o				
S. emphaeus				x	x					x	o						x	o				
S. entomelas				o	x	x					x	o	o				x	o	o			
S. eos[2]	o	x	x						x	o							o	o				
S. flavidus				x	x	o				o	x	o					o	x	o			
S. goodei			o	x							x	o				o	x	o				
S. helvomaculatus		o	x	o					x	o					o	x	o	o				
S. jordani			o	o	o	o					o	x	x	o					x	x	x	o
S. maliger		o	x	x					o	x						o	x					
S. melanops			o	x	x	o				o	x	o						o	x	o		
S. melanostomus		o	x	o	o				o	x	o						o	o	o	o		
S. miniatus			o	x	o				o	x	o					o	o	x				
S. mystinus					x	x	o				x	x	o			o	x	x				
S. nebulosus		o	x	o					o	x	o					o	o	x				
S. nigrocinctus			o	x	o				o	x								o	o	o		
S. paucispinis			o	x	o						o	x	o		x	o						
S. pinniger			o	x	x					x						o	x	o				
S. proriger			o	x	x				o	x						o	x	o				
S. rastrelliger		o	x	o					x									o	o	o		
S. reedi			o	x	x					x	x							o	x	o		
S. rosaceus[2]	o	o	x	o				o	x	o						o	x	o				
S. ruberrimus			o	o	x	o		o	o	x	o							o	x	o		
S. saxicola		o	x	o				o	o	x	o				o	x	o					
S. wilsoni			x	x					x	o						o	x					
S. zacentrus			o	x	x				o	x	o						x	o	o			

[1]Compiled from Phillips (1957), Westrheim (1966), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 4.—Total numbers of gill rakers on first gill arch for rockfishes (*Sebastes* spp.) occurring off Oregon.[1]

Species	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
S. aleutianus									x	x	x	x	x	x												
S. alutus									x	x	x	x	x	x	x	x	x									
S. auriculatus				x	x	x	x	x	x																	
S. aurora			x	x	x	x	x																			
S. babcocki								x	x	x	x	x														
S. borealis						x	x	x	x	x																
S. brevispinis												x	x	x	x											
S. caurinus					x	x	x	x	x	x	x															
S. chlorostictus										x	x	x	x	x	x											
S. crameri								x	x	x	x	x	x													
S. diplopora											x	x	x	x	x	x										
S. elongatus							x	x	x	x	x	x														
S. emphaeus																		x	x	x	x	x	x	x		
S. entomelas													x	x	x	x										
S. eos[2]					x	x	x	x	x	x																
S. flavidus												x	x	x	x	x	x	x								
S. goodei													x	x	x	x	x	x								
S. helvomaculatus							x	x	x	x	x	x														
S. jordani																				x	x	x	x	x	x	x
S. maliger								x	x	x	x	x														
S. melanops												x	x	x	x	x	x	x								
S. melanostomus						x	x	x	x	x	x	x	x	x												
S. miniatus														x	x	x	x	x	x	x	x	x	x			
S. mystinus												x	x	x	x	x	x									
S. nebulosus					x	x	x	x	x	x																
S. nigrocinctus						x	x	x	x	x																
S. paucispinis							x	x	x	x																
S. pinniger																			x	x	x	x	x	x		
S. proriger															x	x	x	x	x	x	x	x				
S. rastrelliger	x	x	x	x																						
S. reedi									x	x	x	x	x	x	x											
S. rosaceus[2]								x	x	x	x	x	x													
S. ruberrimus				x	x	x	x	x	x																	
S. saxicola										x	x	x	x	x												
S. wilsoni																	x	x	x	x	x	x				
S. zacentrus										x	x	x	x	x	x	x										

[1]Compiled from Phillips (1957), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 5.—Numbers of lateral line pores for rockfishes (*Sebastes* spp.) occurring off Oregon.[1]

Species	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
S. aleutianus			x	x	x	x	x	x										x	x	x	x	x	x	x	x	x											
S. alutus																x	x	x	x	x	x	x	x	x	x												
S. auriculatus															x	x	x	x	x	x	x	x															
S. aurora	x	x	x	x	x																																
S. babcocki															x	x	x	x	x	x	x	x															
S. borealis		x	x	x	x	x																															
S. brevispinis																		x	x	x	x	x	x	x	x	x	x										
S. caurinus											x	x	x	x	x	x	x	x	x																		
S. chlorostictus									x	x	x	x	x	x	x	x	x																				
S. crameri														x	x	x	x	x	x	x	x	x	x	x													
S. diploproa							x	x	x	x	x	x	x	x	x	x	x																				
S. elongatus														x	x	x	x	x	x																		
S. emphaeus													x	x	x	x	x	x	x	x	x																
S. entomelas																										x	x	x	x	x	x	x					
S. eos[2]								x	x	x	x	x	x	x	x	x																					
S. flavidus																							x	x	x	x	x	x	x	x	x	x	x	x			
S. goodei																						x	x	x	x	x	x	x	x	x	x	x					
S. helvomaculatus								x	x	x	x	x	x	x	x	x	x	x	x																		
S. jordani																										x	x	x	x	x	x	x	x				
S. maliger									x	x	x	x	x	x	x	x	x	x	x	x	x	x															
S. melanops																				x	x	x	x	x	x	x	x										
S. melanostomus			x	x	x	x	x																														
S. miniatus														x	x	x	x	x	x	x	x																
S. mystinus																		x	x	x	x	x	x	x	x	x	x	x	x	x							
S. nebulosus											x	x	x	x	x	x	x	x	x	x	x	x															
S. nigrocinctus															x	x	x	x	x	x	x	x	x	x													
S. paucispinis																												x	x	x	x	x	x	x	x	x	x
S. pinniger													x	x	x	x	x	x	x																		
S. proriger																					x	x	x	x	x	x	x										
S. rastrelliger																x	x	x	x	x	x																
S. reedi																					x	x	x	x	x	x	x	x	x								
S. rosaceus[2]										x	x	x	x	x	x	x	x	x	x	x																	
S. ruberrimus													x	x	x	x	x	x	x	x																	
S. saxicola										x	x	x	x	x	x	x																					
S. wilsoni											x	x	x	x	x	x	x	x																			
S. zacentrus													x	x	x	x	x	x	x																		

[1]Compiled from Phillips (1957), Westrheim (1966), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 6.—Number of diagonal scale rows below the lateral line for rockfishes (*Sebastes* spp.) occurring off Oregon.[1]

Species	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
S. aleutinaus												x	x	x	x	x	x	x	x	x								
S. alutus														x	x	x	x	x	x	x								
S. auriculatus										x	x	x	x	x	x	x	x											
S. aurora						x	x	x	x	x	x	x	x	x	x													
S. babcocki																												
S. borealis	x	x	x	x	x	x	x	x	x	x	x																	
S. brevispinis																							x	x	x	x	x	x
S. caurinus				x	x	x	x	x	x	x	x	x	x	x	x													
S. chlorostictus								x	x	x	x	x	x															
S. crameri													x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	
S. diploproa																		x	x	x	x	x						
S. elongatus							x	x	x	x	x	x	x	x	x	x	x	x	x	x								
S. emphaeus						x	x	x	x	x	x	x	x	x	x													
S. entomelas																							x	x	x	x	x	x
S. eos[2]						x	x	x	x	x	x	x	x															
S. flavidus																				x	x	x	x	x	x			
S. goodei																									x	x	x	x
S. helvomaculatus							x	x	x	x	x	x	x															
S. jordani																												
S. maliger				x	x	x	x	x	x	x																		
S. melanops															x	x	x	x	x	x								
S. melanostomus										x	x	x	x	x	x													
S. miniatus										x	x	x	x															
S. mystinus															x	x	x	x	x	x	x							
S. nebulosus								x	x	x	x	x	x															
S. nigrocinctus									x	x	x	x	x	x	x	x	x	x										
S. paucispinis																												
S. pinniger								x	x	x	x	x	x	x	x													
S. proriger																				x	x	x	x	x	x			
S. rastrelliger										x	x	x	x	x	x													
S. reedi																										x	x	x
S. rosaceus[2]						x	x	x	x	x	x	x	x															
S. ruberrimus										x	x	x	x	x	x													
S. saxicola								x	x	x	x	x	x	x	x	x	x	x										
S. wilsoni										x	x	x	x	x	x													
S. zacentrus								x	x	x	x	x	x	x	x													

[1]Compiled from Phillips (1957), Westrheim and Tsuyuki (1967, 1972), Chen (1971), Miller and Lea (1972), and Hart (1973), and original data for *S. emphaeus*.
[2]Species may be rare off Oregon.

APPENDIX TABLE 6.—Continued.

Species	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
S. aleutianus																											
S. alutus																											
S. auriculatus																											
S. aurora																											
S. babcocki																											
S. borealis																											
S. brevispinis	x	x	x	x	x	x	x																				
S. caurinus																											
S. chlorostictus																											
S. crameri																											
S. diploproa																											
S. elongatus																											
S. emphaeus																											
S. entomelas	x	x	x																								
S. eos[2]																											
S. flavidus																											
S. goodei	x	x	x	x	x	x	x	x	x	x	x	x	x	x													
S. helvomaculatus																											
S. jordani		x	x	x	x	x	x																				
S. maliger																											
S. melanops																											
S. melanostomus																											
S. miniatus																											
S. mystinus																											
S. nebulosus																											
S. nigrocinctus																											
S. paucispinis									x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
S. pinniger																											
S. proriger																											
S. rastrelliger																											
S. reedi	x	x	x	x																							
S. rosaceus[2]																											
S. ruberrimus																											
S. saxicola																											
S. wilsoni																											
S. zacentrus																											

AERIAL SURVEY OF THE BOTTLENOSED DOLPHIN, *TURSIOPS TRUNCATUS*, AND THE WEST INDIAN MANATEE, *TRICHECHUS MANATUS*, IN THE INDIAN AND BANANA RIVERS, FLORIDA

STEPHEN LEATHERWOOD[1]

ABSTRACT

Aerial surveys were conducted of the Indian and Banana Rivers, eastern Florida, to estimate numbers of bottlenosed dolphins and West Indian manatees. Thirty-nine east-west transects, 4.63 km (2.5 n.mi.) apart, were flown on six successive days in August. Observers at inlets from the ocean inventoried dolphins and manatees entering or leaving the river during the hours of the surveys. There were 64 sightings of dolphins from aircraft, totaling 507 animals. Fifteen dolphins were seen entering or leaving the river. Direction of movement within the inlets appeared unrelated to tidal flow. The population of dolphins in the rivers during the week of the survey (10-15 August 1977) was estimated at 438 ± 127. Calves composed 8.1 to 10.1% of all animals seen. Feeding was observed at widely scattered times and locations. There were 60 sightings of manatees totaling 151 animals. No attempt is made to estimate the size of the manatee population. Calves made up 9.9 to 13.2% of all manatees seen.

The portion of the intracoastal waterway of eastern Florida between about lat. 28°47′N and 27°10′N consists of the connected waters of the Indian and Banana Rivers (Figures 1, 2, 3). Together they form a complex waterway just over 185.0 km (100 n.mi.) long and from <0.93 km (0.5 n.mi.) to >9.3 km (5.0 n.mi) wide. Below the junction of the two rivers at the southern tip of Merritt Island (approximately lat. 28°09′30″N), the Indian River is connected to the adjacent Atlantic Ocean by boating channels at Sebastian and Fort Pierce Inlets.

Like many other portions of the intracoastal waterway, the Indian-Banana River complex is home to Atlantic bottlenosed dolphin, *Tursiops truncatus*. Although the numbers of dolphins inhabiting the rivers is unknown, they have been rumored to contain as many as 5,000 individuals (Orr[2]). Whatever its actual size, however, this population is at the center of a growing controversy. Commercial fishermen in the river and the adjacent ocean report that the dolphins are a nuisance and menace, annually causing an estimated $441,000 worth of damage to longlines and trammel nets used in the Spanish and king mackerel fisheries and not infrequent injury to fishermen (Cato and Prochaska 1976). The fishermen have reportedly requested assistance from the Federal government in controlling the dolphin populations. (White[3]). Recent attempts to use sounds projected underwater to deter the dolphins from approaching fishing nets and boats have had little effect (Caldwell and Caldwell[4]). Because of restrictions imposed on the "taking" of marine mammals by the Marine Mammal Protection Act of 1972, and concerns about the dolphins' roles in the ecosystem, any attempts to reduce the alleged interference of dolphins with the fishing activity must fall under close scrutiny.

The river complex is also home, at least seasonally, to some endangered West Indian manatees, *Trichechus manatus*. The status of these and other manatees of the mainland United States has been most recently reviewed by Hartman[5] and Irvine and Campbell (1978).

During August 1977, I conducted an aerial survey of Indian and Banana Rivers to estimate the size and productivity (number of calves) of the bottlenosed dolphin population. In addition, I took

[1]Biomedical Group, Naval Ocean Systems Center, San Diego, Calif.; present address: Hubbs/Sea World Research Institute, 1700 South Shores Road, San Diego, CA 92109.

[2]Orr, J. M. 1977. A survey of Tursiops populations in the coastal United States, Hawaii and Territorial Waters. Contract Report No. PL92-522, to the U.S. Marine Mammal Commission, Wash., D.C., 18 p.

[3]J. R. White, Doctor of Veterinary Medicine, 16501 S.W. 184th St., Miami, Fla., pers. commun. July 1977.

[4]Caldwell, D. K., and M. C. Caldwell. 1975. Dolphins and fisheries. *In* A report on the Sea Grant program, p. 28-29. State University System of Florida.

[5]Hartman, D. S. 1974. Distribution, status and conservation of the manatee in the United States. Unpubl. rep. in files of U.S. Dep. Inter., Natl. Fish Wildl. Lab., Wash., D.C., 126 p.

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advantage of the survey to count manatees and to note numbers of manatee calves.

MATERIALS AND METHODS

The survey design follows the recommendations of Leatherwood et al. (1978) for a strip census of bottlenosed dolphins. Thirty-nine east-west transects were placed 4.63 km (2.5 n.mi.) apart. Each day for six successive days (10-15 August) the replicate transects were flown in a Cessna 172 Skyhawk[6] travelling 167.0 km/h (90 kn) at an altitude of 150 m (500 ft).

The visual angle which provided 0.463 km (0.25 n.mi.) coverage on each side was determined prior to the survey and marked by tape on the wing struts and windows. One observer on each side searched for dolphins within 0.463 km of the aircraft. Sightings near the outer boundary of the survey strip were checked using an inclinometer. Sightings outside the survey strip and on connecting legs were ignored. Each time dolphins were sighted within the survey strip, the aircraft diverted to the group and circled until the following information could be obtained: location of the sighting (using landmarks and local navigational aids), number of individuals, number of apparent calves of the year, group activity, and swimming direction.

Each time manatees were sighted, both on the survey transects and on the legs connecting transects, the same procedure was followed. Adults and calves were clearly distinguishable (calves were defined as small animals in the close company of a much larger adult). A total of five individuals of a third class, intermediate-sized animals, were logged separately as possible older calves. Because manatees were secondary targets of the survey, less time was generally spent on manatee than on dolphin sightings.

As an index to through-water visibility, records were maintained on 3 days of the percentage of each transect for which the bottom within the strip was visible from the aircraft. To minimize effects of other potential variables on counts the following controls were exercised: all flights were conducted between 0725 and 1300; observers remained the same and maintained the same positions in the aircraft; altitude and speed were held constant; methods of searching and circling were the same throughout; estimates of totals and numbers of calves were agreed upon by observers before each sighting was logged and transects resumed. Surveys were only conducted when the sea surface and winds were estimated to be a Beaufort number of 1.5 or below. Because weather was generally excellent for all 6 days, this required only one 40-min suspension on 14 August to permit a rain squall and associated winds to pass. Each day, during the hours of the aerial surveys, observers stationed on shore logged numbers of dolphins and manatees entering or leaving Indian River by Sebastian and Fort Pierce Inlets and the direction of travel of these animals relative to tidal flow.

Resultant data on dolphins were analyzed following the procedures outlined by Leatherwood et al. (1978) for a strip census of bottlenosed dolphins. Inherent in the application of this method is the critical assumption that all dolphin herds within the 0.926 km (0.5 n.mi.) are observed. Resultant data on manatees are presented as incidental observations with no attempt to estimate population size.

RESULTS

Dolphins

On each replicate of the transects, I surveyed approximately 174.0 linear km (94 n.mi.) or 161.2 km² (47 n.mi.²) of water, an estimated 20% of the surface area of the rivers. In all, 64 sightings of dolphins, totaling 507 animals (Table 1) were made on the transects (Figures 1, 2, 3). Sightings included from 1 to 35 individuals about a mean of 8.2 and a median of 5. The distribution of herd sizes by replicate is shown in Figure 4.

Animals clearly identifiable as calves of the year were seen with 22 groups (34.4%) and comprised 8.1% of all animals seen (Table 1). Slightly larger animals, perhaps older calves of the year,

TABLE 1.—Numbers of herds and individuals of bottlenosed dolphins observed in Indian and Banana Rivers, Fla., during aerial surveys, 10-15 August 1977.

Survey no. (replicate)	Date	Total no. of herds	Total no. of individuals	Total no. of calves of the season
1	10 Aug.	11	90	6 (6.7%)
2	11 Aug.	10	74	7 (9.5%)
3	12 Aug.	16	106	13 (12.3%)
4	13 Aug.	7	49	3 (6.1%)
5	14 Aug.	7	84	6 (7.1%)
6	15 Aug.	13	104	6 (5.8%)
Totals		64	507	41 (8.1%)

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

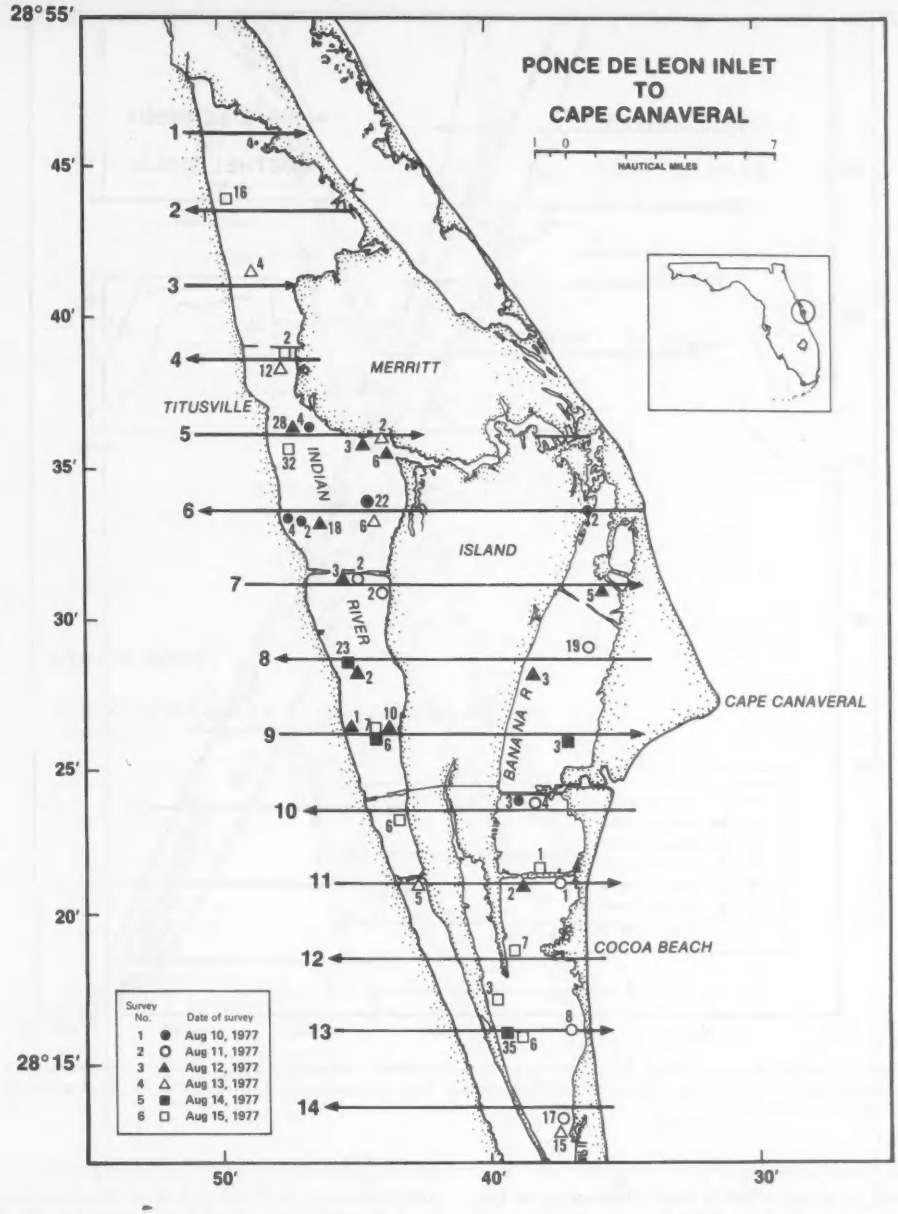

FIGURE 1.—Indian and Banana Rivers, Fla., indicating locations of transects 1-14 and sightings of herds of bottlenosed dolphins. Numbers by the symbols indicate numbers of individuals counted. The symbols indicate locales that were contained within the 0.463-km (0.25 n.mi.) strips.

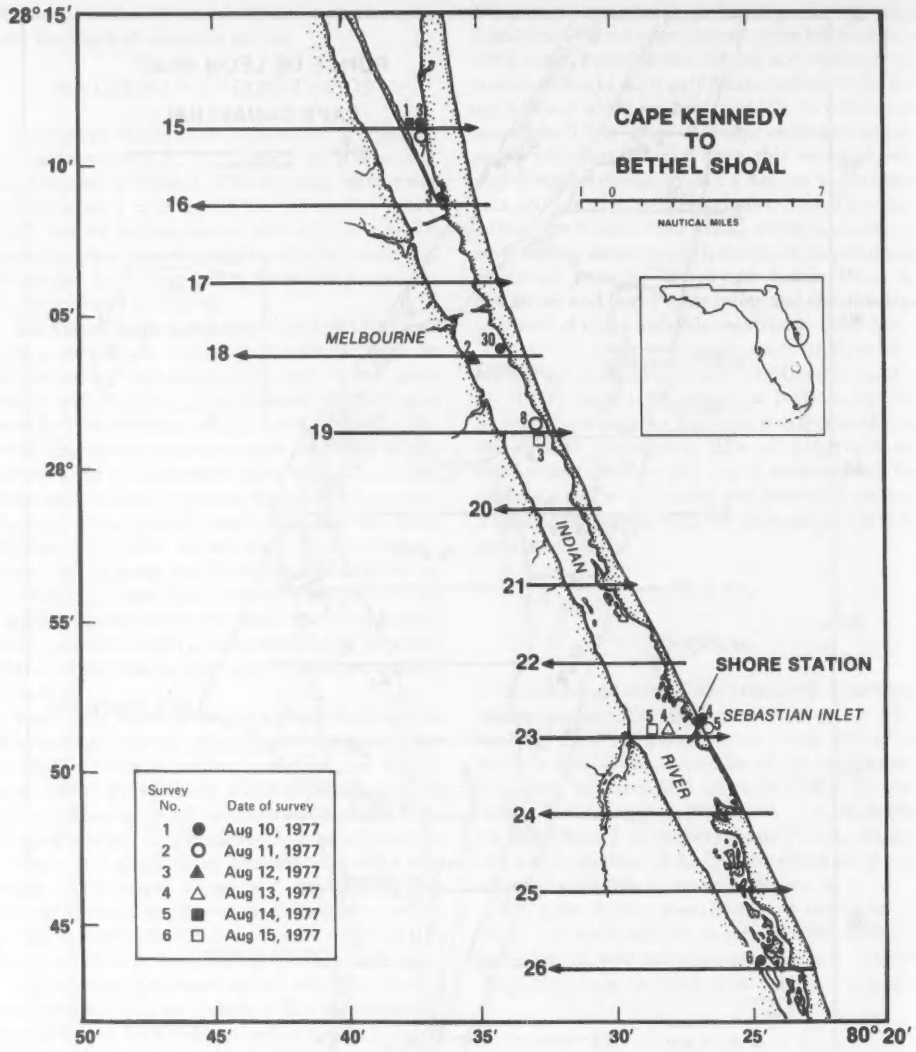

FIGURE 2.—Indian and Banana Rivers, Fla., indicating locations of transects 15-26 and sightings of herds of bottlenosed dolphins. Numbers by the symbols indicate numbers of individuals counted. The symbols indicate locales that were contained within the 0.463-km (0.25 n.mi.) strips.

were seen with seven groups (10.9%) and composed 2% of all animals seen. Depending on the correct classification of these larger animals, total calves of the year surviving at the time of survey appeared to range from 8.1 to 10.1%. The herd densities (number of herds per square kilometer) and mean herd sizes (mean number of animals per herd) for each replicate and the variances of both values are summarized in Table 2. The estimated densities of dolphins were calculated from:

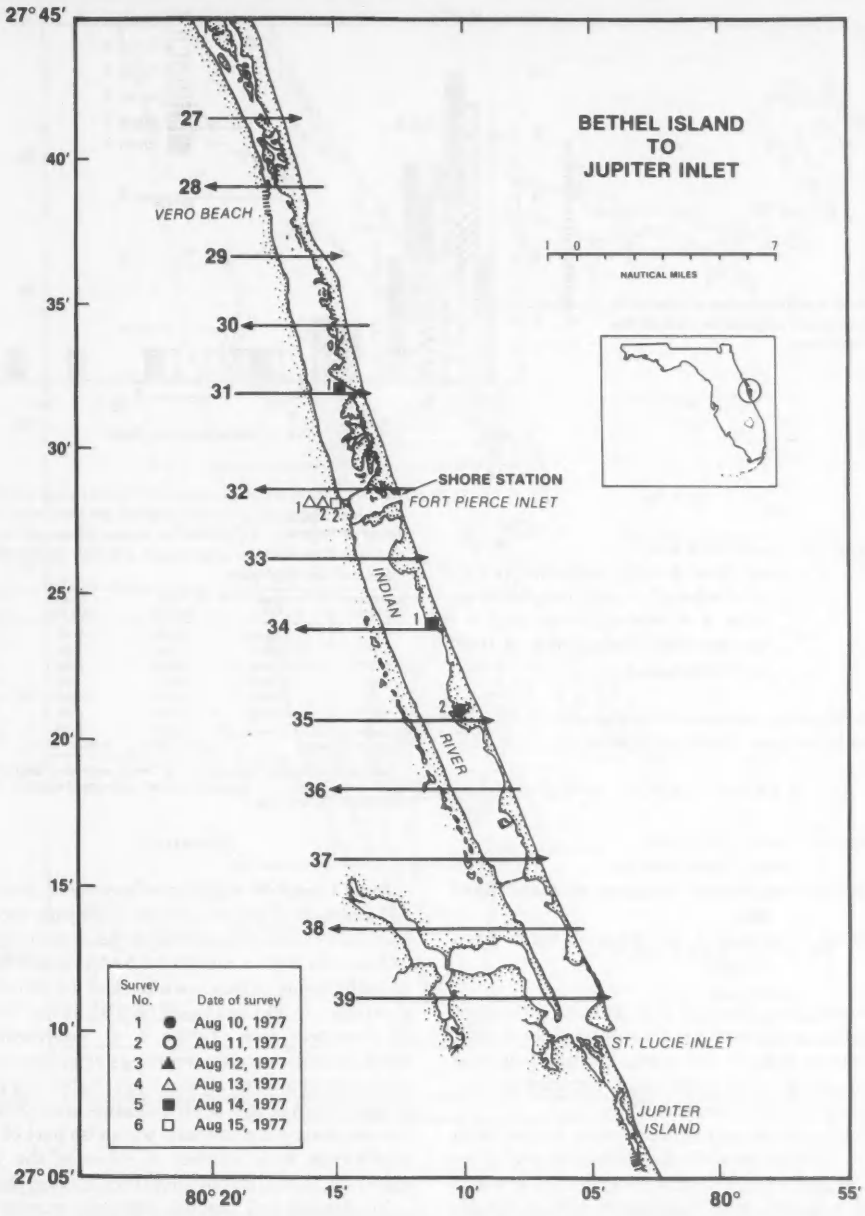

FIGURE 3.—Indian and Banana Rivers, Fla., indicating locations of transects 27-39 and sightings of herds of bottlenosed dolphins. Numbers by the symbols indicate numbers of individuals counted. The symbols indicate locales that were contained within the 0.463-km (0.25 n.mi.) strips.

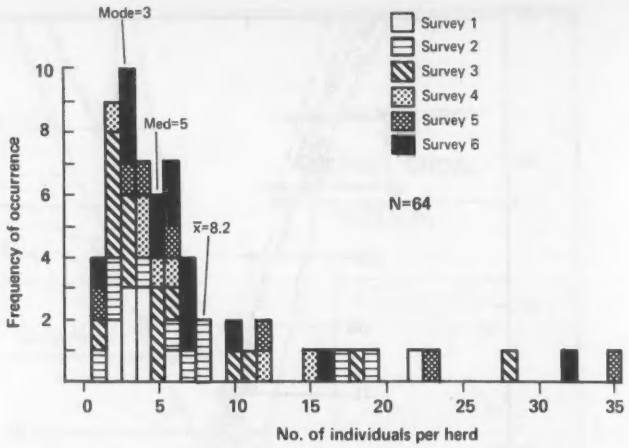

FIGURE 4.—Distribution of herd sizes of bottlenosed dolphins for each of the six replicates.

$$\bar{d} = \bar{h}\bar{a} \quad (1)$$

where $\bar{h}$ = mean herd size
$\bar{a}$ = mean herd density, described as $(\frac{1}{2}L)(n/w)$ where L = total length of transects, n = total sightings, and w = the one-sided strip width of 0.463 km (0.25 n.mi.).

The estimated variance of this product ($S^2(\bar{d})$) was calculated from Goodman (1960):

$$S^2(\bar{d}) = \bar{h}^2S^2(\bar{a}) + \bar{a}^2S^2(\bar{h}) - S^2(\bar{a})S^2(\bar{h}). \quad (2)$$

where $\bar{h}$ = mean herd size
$\bar{a}$ = mean herd density
$S^2(\bar{h})$ = estimated variance of mean herd size
$S^2(\bar{a})$ = estimated variance of mean herd density.

Feeding was observed in portions of 36% (23 of 64) of the groups encountered and was observed in all survey periods and areas. Feeding behaviors were similar to those previously reported for *Tursiops* sp. (Leatherwood 1975).

There was no correlation between the visibility index and the number of sightings on any given transect or set of transects regardless of how data were grouped (rank correlation with Kendall's Tau (Conover 1971) at $\alpha = 0.05$, indicating that significantly larger numbers of animals probably were not missed in the most turbid water).

TABLE 2.—Herd density (number of herds per square kilometer), mean herd size (mean number of dolphins per herd), and dolphin densities (numbers of dolphins per square kilometer) on each replicate. Except where noted means and their variances were calculated over replicates.

Survey no. (replicate)	Date (1977)	Herd density	Mean herd size	Dolphin densities
1	10 Aug.	0.068	8.18	0.556
2	11 Aug.	0.062	7.40	0.459
3	12 Aug.	0.099	6.63	0.656
4	13 Aug.	0.043	7.00	0.301
5	14 Aug.	0.043	12.00	0.516
6	15 Aug.	0.080	8.00	0.640
Means		0.066	8.20	0.521
Variance of means		9.204×10^{-4}	6.35×10^{-1}	0.1837

Using alternate method described in text: Density estimate of dolphins: $\bar{a}\bar{h}$ = 0.542 (from Equation (1)). Variance of density estimate of dolphins: $S^2(\bar{d})$ = 0.094 (from Equation (2)).

Manatees

In all I made 60 sightings of manatees, totaling 151 animals (Figures 5, 6, 7). Sightings ranged from individuals to concentrations of as many as 22 animals with a mean of 2.5. Animals clearly identifiable as calves were part of 14 of the 60 sightings (23.3%) and made up 9.9% (15 of 151) of all manatees seen (Tables 3, 4). Intermediate-sized animals, possibly yearlings or older calves, were part of 5 of the 60 sightings (8.3%) and composed 3.3% (5 of 151) of all manatees seen. If these intermediate-sized animals were also part of this year's crop, total number of calves of the year surviving at the time of the survey may be 13.2%.

No attempt was made to estimate numbers of manatees because all manatees were recorded whether on transects or connecting legs and whether within or outside the transect strip.

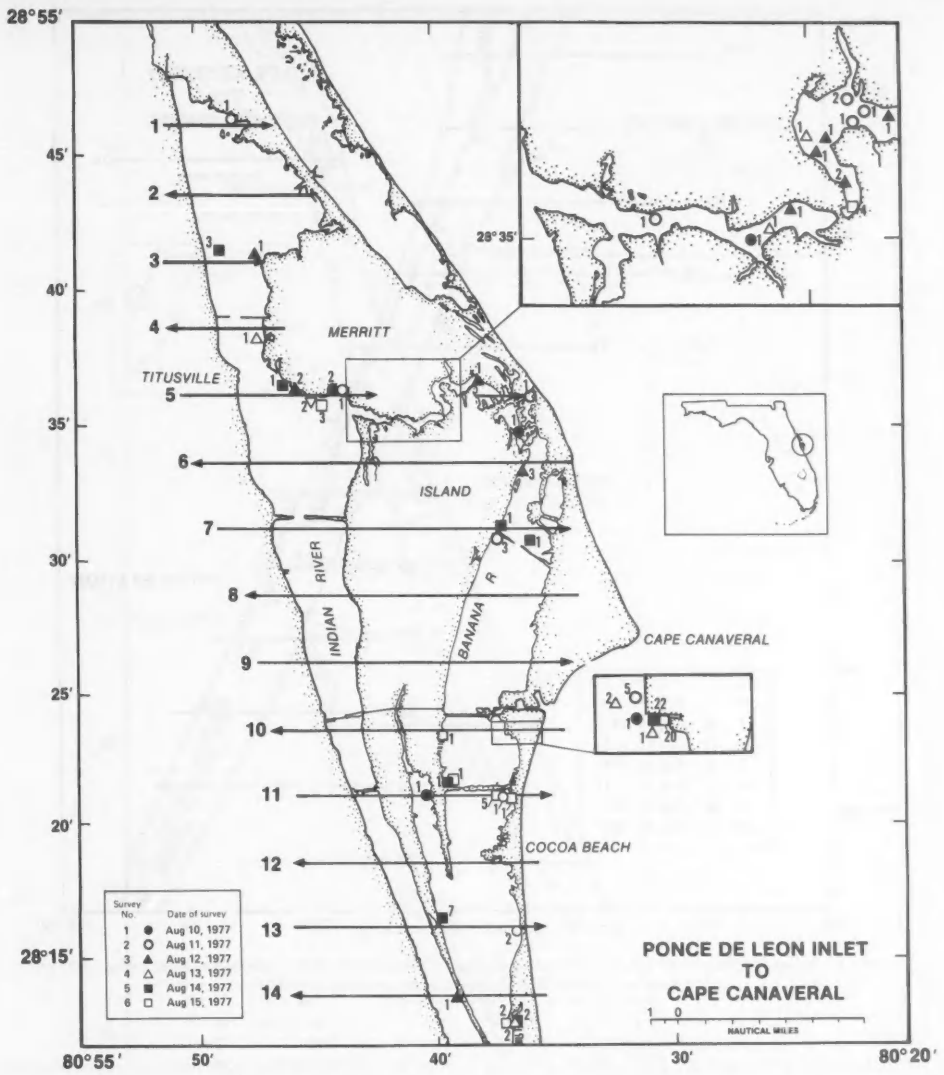

FIGURE 5.—Indian and Banana Rivers, Fla., indication locations of transects 1-14 and sightings of West Indian manatees. Numbers by the symbols indicate estimated numbers of individuals.

Manatees were often observed in several locations (Figures 5, 6, 7) though the numbers counted in each location varied among days.

A single dark adult manatee with a diagonal yellowish slash (perhaps a scar) across the back, seen 12 August near the east end of transect 3 was again observed 13 August, 200 yd from the east end of transect 4.

Manatees were sighted in the inlets on four occasions during the survey (Table 3), a group of two

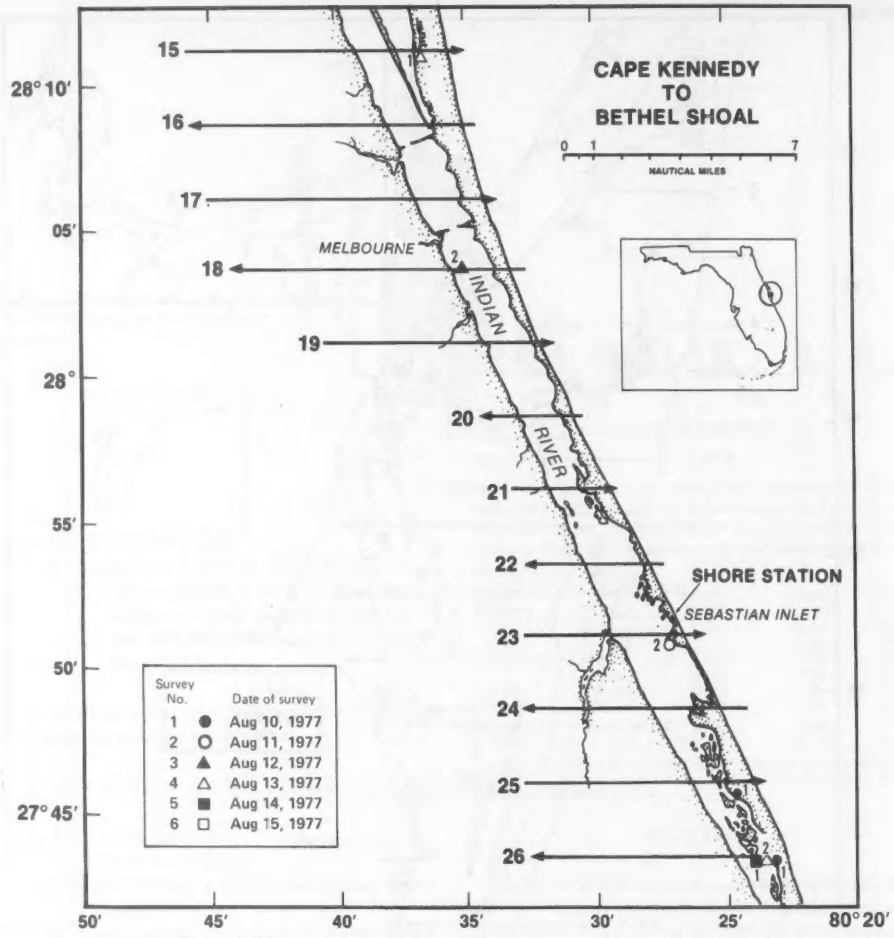

FIGURE 6.—Indian and Banana Rivers, Fla., indication locations of transects 15-26 and sightings of West Indian manatees. Numbers by the symbols indicate estimated numbers of individuals.

animals milling within Fort Pierce Inlet, a group of two adults moving against the tide, and two separate individuals moving with the tide.

Like the dolphins', manatees' movements appeared unrelated to tidal flow within the channels.

DISCUSSION

Dolphins

The estimated number of dolphins in the river at the time of the survey (438 ± 127) was considerably smaller than one would have expected for the area based on the accounts of Cato and Prochaska (1976) and Orr (see footnote 2) and on discussions with fishermen and other residents of the area. However, the densities of dolphins observed were generally much higher than those reported from aerial surveys of the waters of Alabama, Mississippi, and Louisiana (Leatherwood et al. 1978) and the west coast of Florida (Odell and

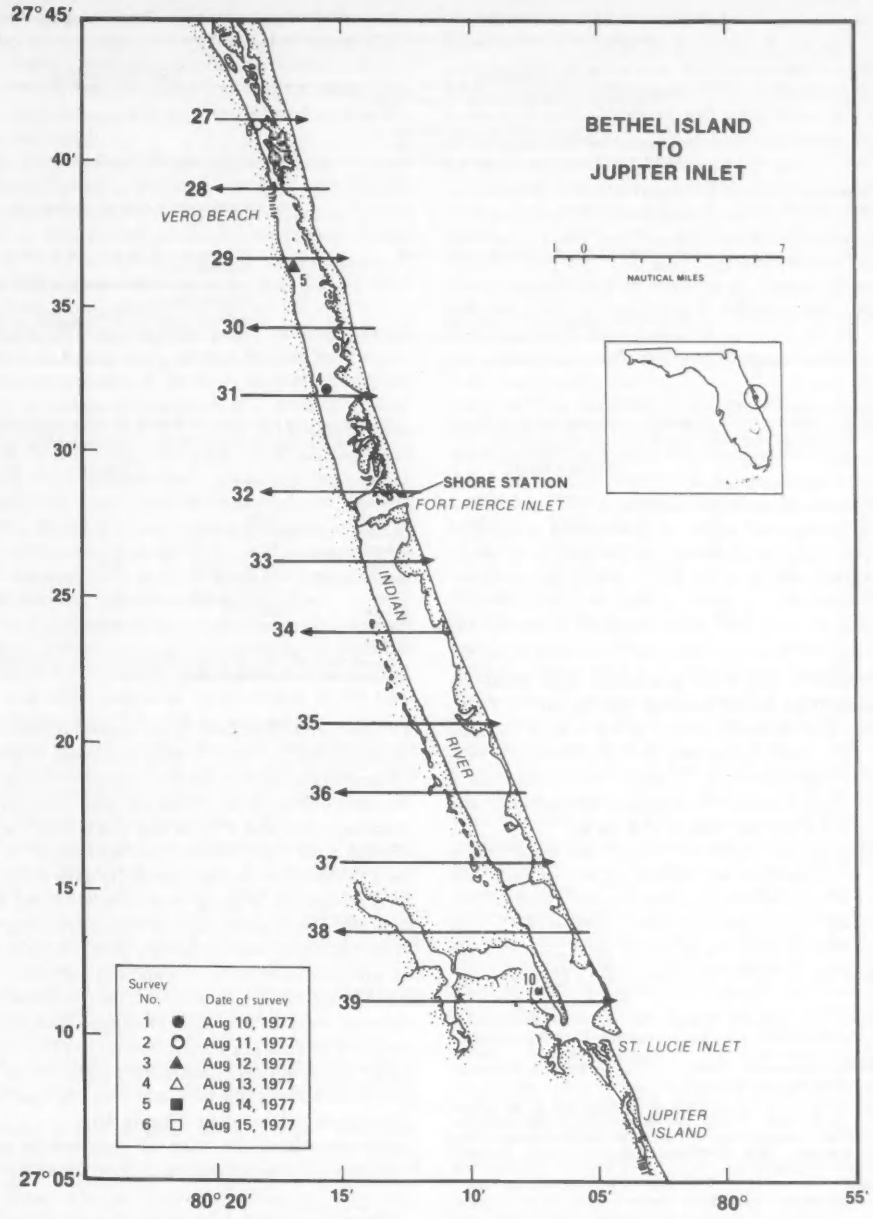

FIGURE 7.—Indian and Banana Rivers, Fla., indicating locations of transects 27-39 and sightings of West Indian manatees. Numbers by the symbols indicate estimated numbers of individuals.

TABLE 3.—Numbers of bottlenosed dolphins and West Indian manatees entering or leaving the Indian River during the time of the aerial surveys, indicating direction of travel relative to tidal flow.

Date (1977)	Bottlenosed dolphins	West Indian manatees
10 Aug.	4 adults moving against tide into river through Sebastian Inlet 7 adults, 2 calves moving with tide from river into Sebastian Inlet thence against tide back into river	0
11 Aug.	1 adult moving against tide into river through Sebastian Inlet	2 adults milling within Fort Pierce Inlet
12 Aug.	0	0
13 Aug.	0	2 adults moving against tide into river through Fort Pierce Inlet
14 Aug.	0	0
15 Aug.	1 "juvenile" milling within Sebastian Inlet at slack tide	1 adult moving with tide from river to ocean through Sebastian Inlet 1 adult moving with tide from river to ocean through Sebastian Inlet
Total	15 individuals, consisting of 5 moving against tide, 9 moving both with and against tide, and 1 milling within inlet	6 individuals, consisting of 2 milling within inlet, 2 moving against tide, and 2 moving with tide

TABLE 4.—Summary of West Indian manatee sightings by day during the six 1-day aerial surveys, August 1977.

Date	Survey no.	Total no. of sightings	Number of animals		
			Total	Calves of season	Other possible calves
10 Aug.	1	9	13	1(7.6%)	1(0.7%)
11 Aug.	2	12	21	2(9.5%)	1(0.7%)
12 Aug.	3	8	18	2(11.1%)	0(—)
13 Aug.	4	11	18	1(5.6%)	0(—)
14 Aug.	5	11	41	5(12.2%)	0(—)
15 Aug.	6	9	40	4(10.0%)	3(2.0%)
Total		60	151	15(9.9%)	5(3.3%)

TABLE 5.—Some estimates of density of bottlenosed dophins, *Tursiops* sp., in coastal waters of the southeastern United States.

Location	Reference	Dolphin per km²	Dolphins per n.mi.²
Mississippi gulf coast	Leatherwood et al. (1978)	0.23	0.57
Louisiana gulf coast	Leatherwood et al. (1978)	0.44	1.08
Florida[1] West Coast	Odell and Reynolds (see footnote 7)	0.23	0.57
Texas gulf coast	Barham et al. (see footnote 8)	0.65	1.61
Florida Indian River	This paper	0.68	1.77

[1]Derived from their Table 10 by computing the product of mean herd size (5.43) and mean herd density (0.0497).

Reynolds[7]), and were consistent with those reported from aerial surveys conducted in Texas using similar methodology (Barham et al.[8]) (Table 5). This consistency and the relatively low variance estimates are evidence that this was a realistic estimate of the numbers of dolphins in the rivers during the time of the survey.

Bottlenosed dolphins have been observed to occur as individuals and in groups of over 200 animals (Leatherwood and Platter[9]). Mean herd sizes of bottlenosed dolphins off eastern Florida and in the Gulf of Mexico vary considerably from one area to another. Groups apparently decrease in size with distance from shore (Odell and Reynolds see footnote 7); tend in coastal waters to be larger in deeper and in open water areas than in shallow embayments, lagoons, and marshlands (Leatherwood and Platter see footnote 9; Leatherwood et al. 1978; Shane and Schmidley[10]); and tend to fluctuate in size seasonally with little pattern discernible (Shane and Schmidley see footnote 10). The mean group size observed during this study (8.2) was well within the limits reported by all authors for eastern Florida and gulf coast waters. This and the lack of correlation between herd size and herd density further support the reasonableness of this population estimate (only if the distribution of herd sizes were normal could the inference technically be made that the two variables were independent (Figure 4)).

Because the estimation of variance in total numbers of animals assumes that herd size and

[7]Odell, D. K., and J. E. Reynolds III. In press. Distribution and abundance of the bottlenosed dolphin, *Tursiops truncatus*, on the west coast of Florida. Contract Report to the U.S. Marine Mammal Commission, Wash., D.C., 55 p. National Technical Information Service, Wash., D.C.

[8]Barham, E. G., J. C. Sweeny, S. Leatherwood, R. K. Beggs, and C. L. Barham. 1978. Aerial census of bottlenosed dolphins (*Tursiops truncatus*) in a region of the Texas coast. Unpubl. manuscr., 34 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[9]Leatherwood, S., and M. F. Platter. 1975. Aerial assessment of bottlenosed dolphins off Alabama, Mississippi, and Louisiana. *In* D. K. Odell, D. B. Siniff, and G. H. Waring (editors), *Tursiops truncatus* assessment workshop, p. 49-86. Final Report, U.S. Marine Mammal Commission, Contract MM5AC021.

[10]Shane, S. H., and D. J. Schmidley. In press. Population biology of Atlantic bottlenosed dolphins, *Tursiops truncatus*, in the Aransas Pass area of Texas. Contract Report to the U.S. Marine Mammal Commission, Wash., D.C., 238 p. National Technical Information Service, Wash., D.C.

herd density are mutually independent, the data by day were examined for correlation. Using Kendall's rank correlation coefficient (Conover 1971) at $\alpha = 0.05$, mean herd size and mean herd density were demonstrated to be uncorrelated within the area surveyed.

The dolphin densities per square kilometer were then multiplied by the area surveyed and a factor of 5 (since the survey covered 20% of the total area) and the 95% confidence limits calculated for the estimate. The figures support an estimate of 438 ± 127 dolphins for the Indian and Banana Rivers during the time of the survey.

As an alternate method for estimating dolphin densities, I took the average density over replicates from column 3, Table 2. This procedure results in a density estimate of 0.40 dolphin/km^2 (1.36 dolphins/n.mi.^{2}), a value very close to the estimate obtained using the method described above (0.41 dolphin/km^2, 1.41 dolphins/n.mi.^{2}), but having a variance twice as large (0.1837 vs. 0.094). Because of the higher variance, it can be argued that the first method used, because it takes into account both average herd size and average herd density, is preferable in this case.

The numbers of dolphins entering or leaving the river at Sebastian (4 groups totaling 15 animals) and Fort Pierce Inlets (none sighted) were negligible and were judged as insignificant to the total population size. Two of those groups were entering the river against an outgoing tide, one moved from the river into the inlet on an ebbing tide, then turned around and reentered the river, and one was milling within the inlet (Table 3).

The surprisingly low estimate does, of course, raise an important question. Is the population of bottlenosed dolphins in the river complex always this small (and only appears larger because of periodic concentrations of animals in limited areas) or is it augmented seasonally by influxes of animals from other areas migrating into the rivers in response to the movement of fishes?

Caldwell (1955) and others have suggested limited home ranges for bottlenosed dolphins. Wells et al.,[11] Irvine et al.,[12] and Shane and Schmidley (see footnote 10) have all clearly demonstrated limited home ranges for portions of the populations in their study areas; Wells et al. (see footnote 11) have shown differences in size and locations of home ranges based on age and sex classes, and all these authors have reported some movements of animals into and out of their study areas.

Caldwell and Caldwell (1972) summarize the views of the fishermen from eastern Florida that there are "river" and "ocean" *T. truncatus* populations. Caldwell et al. (1975) presented evidence from the distribution of cases of "Lobos" disease (lobomycosis) in bottlenosed dolphins that indicate greatest susceptibility to the disease in riverine-estuarine stocks and suggest isolation of river from ocean stocks.

Shane[13] reported that the offshore population of bottlenosed dolphins off Texas rarely interacted with the bay population but that the winter population in the Port Aransas area was at least twice as large as that in summer, because the bay population was augmented by "large numbers" of dolphins entering that area for the winter either from the adjacent gulf or from adjacent bay systems. Whether or not a similar influx occurs in the Indian River is unclear. Additional surveys during the peak seasons of the most important midwinter fisheries (king and Spanish mackerel, bluefish, spots, and pompano) might provide answers.

In considering the questions of the dolphins' population size and alleged damage to nets, it should be remembered that bottlenosed dolphins, at least in some areas, are not uniformly distributed but tend to concentrate in areas of high fish productivity (Leatherwood and Platter see footnote 9) which are often areas of highest human use (Leatherwood 1975). Irvine et al. (see footnote 12), for example, reported that short-term movements of bottlenosed dolphins near Tampa Bay appear to correlate with movements of mullet. Frequent joint use of resources by dolphins and humans make the dolphins highly visible and could result in inflated estimates of their numbers.

Even if not augmented seasonally by immigration from other areas, the relatively small dolphin population in Indian and Banana Rivers could be responsible for net damage of the types reported by Cato and Prochaska (1976). Feeding by dolphins near seine and gill net fisheries is well known

[11]Wells, R. S., A. B. Irvine, and M. D. Scott. 1977. Home range characteristics and group composition of the Atlantic bottlenosed dolphin *Tursiops truncatus* on the west coast of Florida. *In* Proceedings (Abstr.) of the Second Conference on the Biology of Marine Mammals, San Diego, Calif., 12-15 Dec. 1977, p. 15.

[12]Irvine, A. B., M. D. Scott, and R. S. Wells. 1977. Movements and activities of Atlantic bottlenosed dolphins. *In* Proceedings (Abstr.) of the Second Conference on the Biology of Marine Mammals, San Diego, Calif., 12-15 Dec. 1977, p. 16.

[13]Shane, S. H. 1977. Population biology of *Tursiops truncatus* in Texas. *In* Proceedings (Abstr.) of the Second Conference on the Biology of Marine Mammals, San Diego, Calif., 12-15 Dec. 1977, p. 57.

(Leatherwood 1975), and dolphins sometimes become entangled as a consequence (Mitchell 1975). An entangled adult dolphin, struggling for escape, is certainly capable of ripping a small-mesh net apart. Further, bottlenosed dolphins have been documented stealing fish from longlines (Iverson[14]). Even so, dolphins may not actually be responsible for all or even the majority of the damage in Indian River. Cato and Prochaska (1976) refer to damage to nets by sharks and cite the need for deterrents. D. K. Caldwell[15] reviewed the evidence and concluded that the majority of damage to nets in the Indian River was probably caused by sharks and not by dolphins, citing as support numerous reports by fishermen and others working the area of sharks around nets. He also concluded, however, that dolphins were stealing fish and damaging gear in the king mackerel fishery in the nearby Atlantic Ocean. During the aerial surveys, I observed huge concentrations of sharks on the sand bars at the entrance of St. Lucie Channel. Therefore, the question of what causes the damage to nets is still open and regulation of the dolphin population based on its supposed size and levels of damage to the fisheries would be premature.

Irvine et al. (see footnote 12) reported that in spring calves composed as much as 14% of the bottlenosed dolphin population near Tampa Bay. Shane (see footnote 13) reported that calves constituted from 3.65% (February) to 12.92% (May) of the dolphins in the Port Aransas area ($\bar{x}$ = 7.61); Leatherwood et al. (1978) reported summer figures from 7.7 to 7.9% calves for coastal Alabama, Mississippi, and Louisiana. The 8.1-10.1% calves observed during this survey therefore are well within the reported ranges of percentages of calves in local bottlenosed dolphin populations.

It has been noted that in areas where tidal flow is negligible, as is the case within these rivers, dolphin movements appear to be related to some factor other than tide (Shane and Schmidley see footnote 10). Shane and Schmidley found that the dolphins in areas of swiftest current moved against tidal flow. The inability to ascertain a relationship between swimming direction of groups and tidal flow in the river inlets in this study is perhaps related to our small sample size.

Manatees

Hartman (see footnote 5) and Irvine and Campbell (1978) reported that Florida manatees concentrated near warmwater refugia during winter months but dispersed during the remainder of the year. The 151 manatees (some no doubt repeats on successive days) sighted during this survey were distributed throughout the nearshore waters of the Indian-Banana River complex, including several less saline canals, and animals were not concentrated near the St. Lucie power station or other potential warmwater areas where winter concentrations have been reported (Irvine and Campbell 1978). No manatees were observed in the deeper open water of the rivers. All were in shallower coastal waters, marinas, creek mouths, bayous, and canals. The number of calves observed, composing from 9.9 to 13.2%, depending on the correct classification of the intermediate-sized animals observed, falls within the ranges of 9.6% calves (winter) and 13.4% calves (summer) reported by Irvine and Campbell (1978).

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DEVELOPMENT OF PELAGIC LARVAE AND POSTLARVA OF *SQUILLA EMPUSA* (CRUSTACEA, STOMATOPODA), WITH AN ASSESSMENT OF LARVAL CHARACTERS WITHIN THE SQUILLIDAE

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ABSTRACT

Larvae of the predatory crustacean *Squilla empusa* were collected from the plankton in Chesapeake Bay and reared in the laboratory to permit description of the pelagic stages before the postlarval stage.

Characters such as rostral length and spinulation, carapace spinulation, relative size of telson, overall body size, and appearance probably are of more value for specific than for generic identification. The presence or absence of teeth on the dactylus of the second maxilliped, the presence or absence of a spine on the basis of the second maxilliped, and the number of epipods may be useful characters in determining generic alliances of larvae belonging to the Squillidae, but present data are not adequate for construction of generic keys to stomatopod larvae.

Mantis shrimps are formidable predators, able to slice a swimming shrimp in half or smash open a bivalve with enlarged second maxillipeds (MacGinitie and MacGinitie 1968). Even though the strike occurs under water, it is one of the fastest movements known in the animal kingdom taking 4 to 8 ms to complete and traveling at a velocity of 1,000 cm/s (Burrows 1969). Basically, any animal of appropriate size may fall prey to a stomatopod including fish, shrimp, crabs, annelids, clams, mussels, snails, squids, and echinoderms (Piccinetti and Manfrin 1970).

Stomatopod larvae are often met with in great swarms, particularly in tropical waters. The planktonic larval stages constitute a considerable portion of the diet of reef fishes and commercially important pelagic fishes such as the tunas, skipjack tuna, mackerel, herring, and snapper (Sunier 1917; Fish 1925; Reintjes and King 1953; Randall 1967; Dragovich 1970).

Squilla empusa Say 1818 is found in the western Atlantic Ocean and ranges from Massachusetts, U.S.A. to northern South America, including Trinidad, Venezuela, Surinam, and French Guiana (Manning 1969). It is abundant throughout its range, but is especially prevalent in commercial shrimp beds, and is believed to be a serious predator of the shrimp. Hildebrand (1954) observed that it is the most abundant crustacean in the offshore trawl fishery of the Gulf of Mexico except for *Penaeus* sp. and *Callinectes* sp. Stomatopods are fished and eaten in most Mediterranean countries, Japan, and the tropical Pacific (Kaestner 1970).

Like the adult, the larvae of *S. empusa* are rapacious predators. Able to attain a length of 17 mm, they can capture zooplankters as large as themselves by using their second maxillipeds (Lebour 1924). *Squilla empusa* larvae not only fill a role as predators, but also as prey. To date very little has been published on the ecology of the larvae nor has the sequence of pelagic stages been established for this species.

Of the 350 known species of stomatopods, only 1 in 10 can be identified with their larvae and only 1 has been reared from hatching to metamorphosis. Difficulty in rearing the larvae has forced investigators to base their accounts on reconstructions made from preserved specimens or from holding planktonic larvae through one ecdysis to connect successive stages. The species of stomatopods for which larvae are definitely known by the rearing of late stage larvae through metamorphosis were listed by Provenzano and Manning (1978). Stomatopod species for which larvae are definitely known by the hatching of eggs also are listed by Provenzano and Manning.

The only description of the developmental sequence of *S. empusa* was made almost 100 yr ago by Brooks (1878) who captured larvae at Fort Wool near the mouth of the Chesapeake Bay. Because

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none of Brooks' larvae metamorphosed into postlarvae, he could not be sure of their identity. However, of the thousands he collected, all appeared to Brooks to be "specifically identical" and the series of forms were so complete with the differences between the successive stages so slight that he concluded there was "no reason to doubt that they are all of the same species, and that species the only one which is known to occur in the Chesapeake Bay." However, we now know that early larval stages of at least one other species of stomatopod occur at the mouth of Chesapeake Bay (Provenzano and Goy, pers. obs.) Brooks' description is inadequate to permit stages to be adequately assigned to larvae.

Brooks apparently was unable to obtain successful molting in his larvae, but instead had to rely on reconstruction to describe the larval history. He provided no conjecture as to the number of pelagic stages, and only partially described four stages. Furthermore, the illustrations which Brooks included were of whole specimens only; detailed figures of appendages, necessary for accurate species identification, were not made.

Faxon (1882), working in Rhode Island, held what he considered to be the last pelagic stage of *S. empusa* until it metamorphosed and could be identified. However, the last stage larva and postlarva appear to belong to another species, not *S. empusa* (see Discussion).

In this paper we describe the pelagic larval development and postlarval stage of *S. empusa*. Because egg masses were not collected, hatched, and reared, the propelagic stages remain undescribed. Furthermore, because larvae were obtained from the plankton, we are not positive that the larvae described as stage I are the true first pelagic stage. However, of the hundreds of larvae collected these stage I larvae are the least developed and closely resemble stage I larvae of other species reared from eggs.

A brief review of previous efforts to associate stomatopod larvae with adults and a discussion of possible specific and generic larval characters within the Squillidae is presented.

METHODS

Larval specimens of *S. empusa* were collected weekly 1 to 2 km north of Cape Henry at the mouth of the Chesapeake Bay where we have determined that a population of adults exists. A ½-m plankton net (153-μm mesh) was used to make 10-min stepped oblique tows, as the ship circled the collection site at idle speed.

Each plankton sample was placed into one or two 1.9-l (½-gal) jars filled with seawater until stomatopod larvae could be separated from the sample. Separation of larvae from the samples was started aboard ship and completed in the laboratory. Larvae were sorted according to size to minimize cannibalism, and held temporarily in aerated 1.9-l jars filled with seawater.

The larvae were then placed in compartmentalized plastic trays, one per compartment. Each tray contained 18 compartments measuring 4.5 × 5 × 4 cm. Medium for rearing the larvae was made from Instant Ocean Synthetic Sea Salts[2] (Aquarium Systems, Inc., Eastlake, Ohio) and tapwater.

Larvae were reared over a range of temperatures (10° to 25°C) and salinities (10 to 35‰) in an attempt to insure survival of at least some larvae since optimum conditions were unknown. Because the larvae were not hatched in the laboratory under the temperature-salinity combination at which they were reared, some larvae had to be acclimated to the test conditions. Lavae were never acclimated to temperature changes of more than 5°C and 10‰/day. The larvae were maintained in total darkness except for brief periods (15 to 20 min/day) when they were examined and transferred to newly prepared trays.

Each larva was reared in 25 ml of water and given approximately 30 *Artemia salina* nauplii/ml daily. Decapod larvae and *A. salina*, grown on yeast or an algal culture of *Dunaliella*, were fed to larvae that became too large to capture or obtain substantial nutrition from the *A. salina* nauplii. Larvae were transferred daily, early stages by means of a pipette, later stages with a spoon, into compartments containing freshly prepared seawater and food. During this transfer, frequency of molting, duration of larval development, survival, and the stage of development were recorded. Dead larvae were preserved in 70% ethyl alcohol and 10% glycerin. Preserved larvae were heated in a 5% potassium hydroxide solution to dissolve the tissue so that only the exoskeleton remained. The larvae were then stained in acid fuchsin red to facilitate description and illustration. Larvae and exuviae were dissected in lactic acid. All larval appendages were illustrated using a Tasco camera lucida on a Unitron binocular compound scope,

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

while the postlarval appendages were illustrated with the aid of a Bausch and Lomb microprojector.

The descriptions of all larval stages were based on five specimens; four specimens were used to describe the postlarva. Carapace length (CL) indicates the distance from the tip of the rostrum to the median posterior margin of the carapace, exclusive of the median spine; telson length (tL), distance from the articulation with the sixth abdominal somite to the median posterior margin of the telson. The term pleotelson (Kaestner 1970) is used to refer to the telson before the sixth abdominal somite has become completely articulated. Pleotelson length (PL) indicates the distance from the articulation with the fifth abdominal somite to the median posterior margin of the pleotelson; telson width (TW) and pleotelson width (PW), distance across the widest portion; rostral length (RL) of the larva, distance from the tip of the rostrum to the base of the anterolateral spines of the carapace; rostral length of the postlarva, distance from the tip of the rostrum to the posterior margin of the rostrum; rostral width (RW) of the postlarva, distance from the tip of the rostrum to the median posterior margin of the telson; and total length (TL) of the postlarva, distance from the anterior margin of the rostrum to the median posterior margin of the telson.

Maxillules, maxillae, pleopods, distal spinules of the rostrum, and most epipods were omitted from illustrations of the whole animal for the sake of clarity.

RESULTS

The pelagic larval development of *S. empusa* was found to include nine stages before the postlarval stage. Juvenile stages reared for several months after metamorphosis attained sizes of approximately 30 to 40 mm TL and could be positively identified with the adult. Although none of the 576 larvae reared at the 16 different temperature and salinity combinations was reared through the entire pelagic development to metamorphosis, larvae survived well and molted frequently at two of the test combinations. Of larvae kept at 20°C, 25‰ salinity, or at 25°C, 25‰ salinity, 47% molted three or more times, 24% underwent at least five ecdyses, and 3% molted seven times over a 6-wk period. Thirty-four animals molted to postlarva. Great increases in size from the first to the last stage necessitated adjustments in food size and quantity. Detailed results of effects of various experimental conditions are being prepared by Morgan for publication elsewhere.

The difficulty in rearing the larvae through the lengthy pelagic development made it necessary to reconstruct the developmental sequence by observing the larvae molt through successive stages.

Stage I (Figure 1A)

Measurements (mm): RL, 0.70 to 1.10; PL, 0.4 to 0.8; TL, 2.9 to 3.3; CL, 0.80 to 1.30; PW, 0.3 to 0.6.

Rostrum deflexed, extending slightly beyond antennular flagella, ventral spinules absent.

Carapace with one pair of supraorbital spines. Lateral margins of carapace convex, armed ventrally with four spinules. Posterior margin of carapace deeply notched, armed with a median dorsal spine. Posterolateral spines, armed with one ventral spinule, extending to fourth abdominal somite.

Ocular somite articulated, armed with one spine on median ventral margin. Antennular somite not articulated.

Antennule (Figure 2A) with long two-segmented inner flagellum, apical segment armed with one strong and one weak seta distally and a pair of weak setae medially, proximal segment armed with one strong and two weak setae distally. Outer flagellum armed with one large and one small seta distally, followed by one weak seta and six aesthetascs arranged 1-2-3 along inner margin. Median flagellum absent.

Antenna (Figure 3A) armed with nine plumose setae, endopod absent.

Mandible (Figure 4A) serrate, mandibular palp absent.

Maxillule (Figure 5A) with coxal endite bearing three spinules and one seta, basal endite with one strong tooth flanked by two strong setae, palp with one long seta, endopod absent.

Maxilla (Figure 6A) unsegmented, armed with six setae.

First maxilliped (Figure 7A) with dactylus small, pointed. Propodus with two extremely minute spinules, inner margin bearing seven strong setae arranged 2-3-2. Carpus with one strong seta distally, merus without setae, epipod absent.

Second maxilliped (Figure 8A) large, basis with stout proximal spine. Propodus with 1 strong terminal tooth followed by 17 to 20 denticles on inner margin. Dactylus armed with spinules, distal

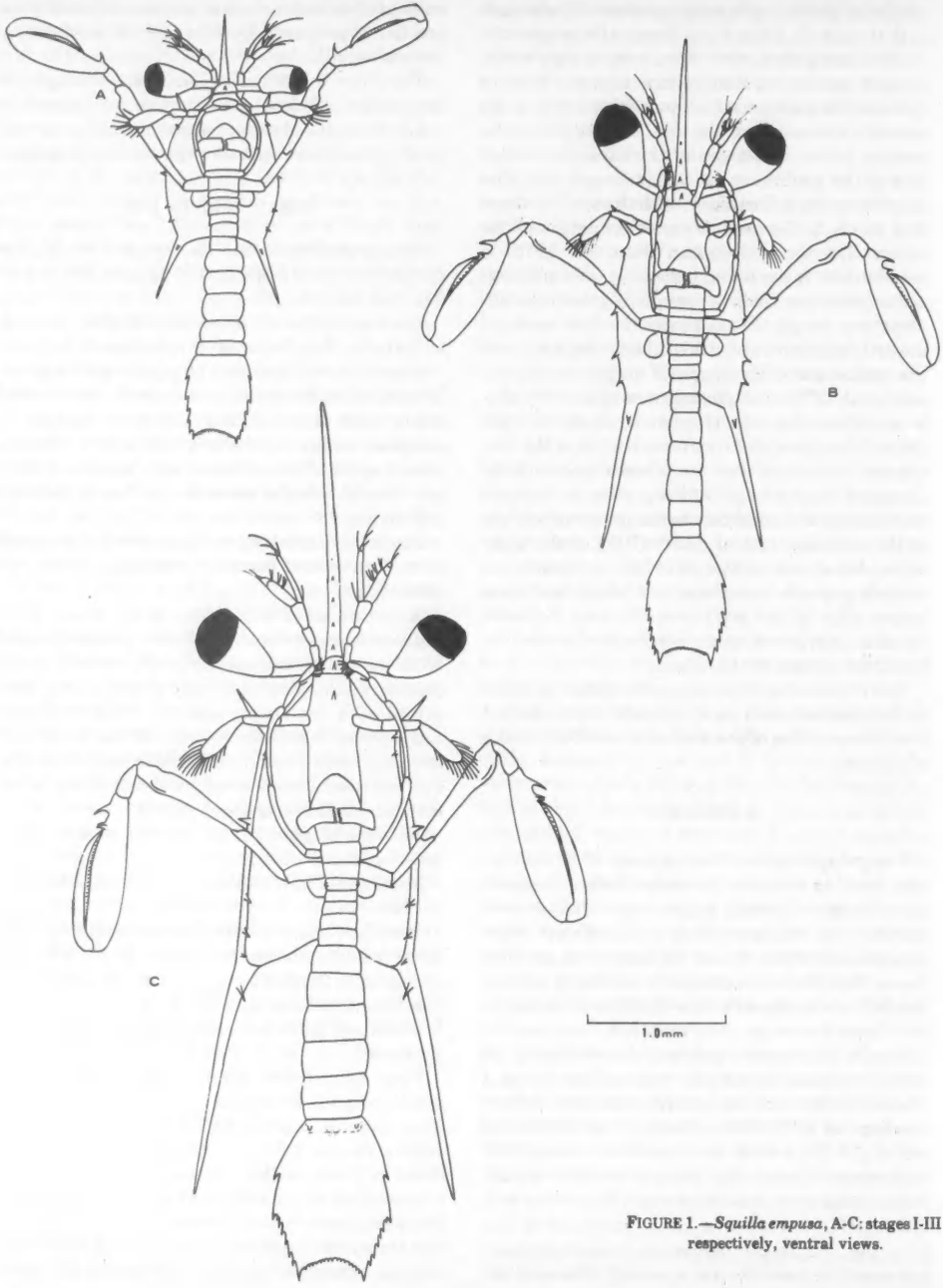


FIGURE 1.—*Squilla empusa*, A-C: stages I-III respectively, ventral views.

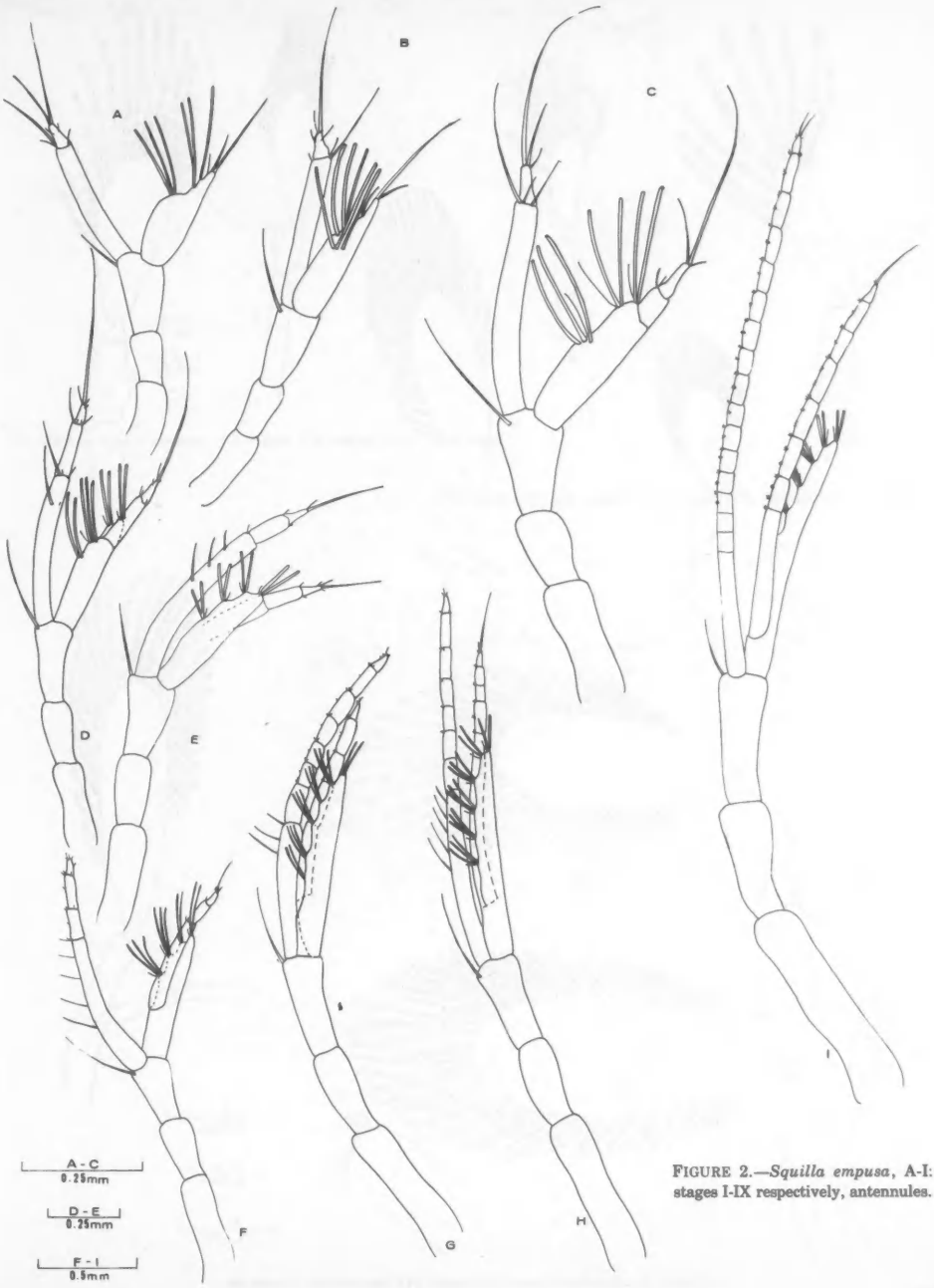


FIGURE 2.—*Squilla empusa*, A-I: stages I-IX respectively, antennules.

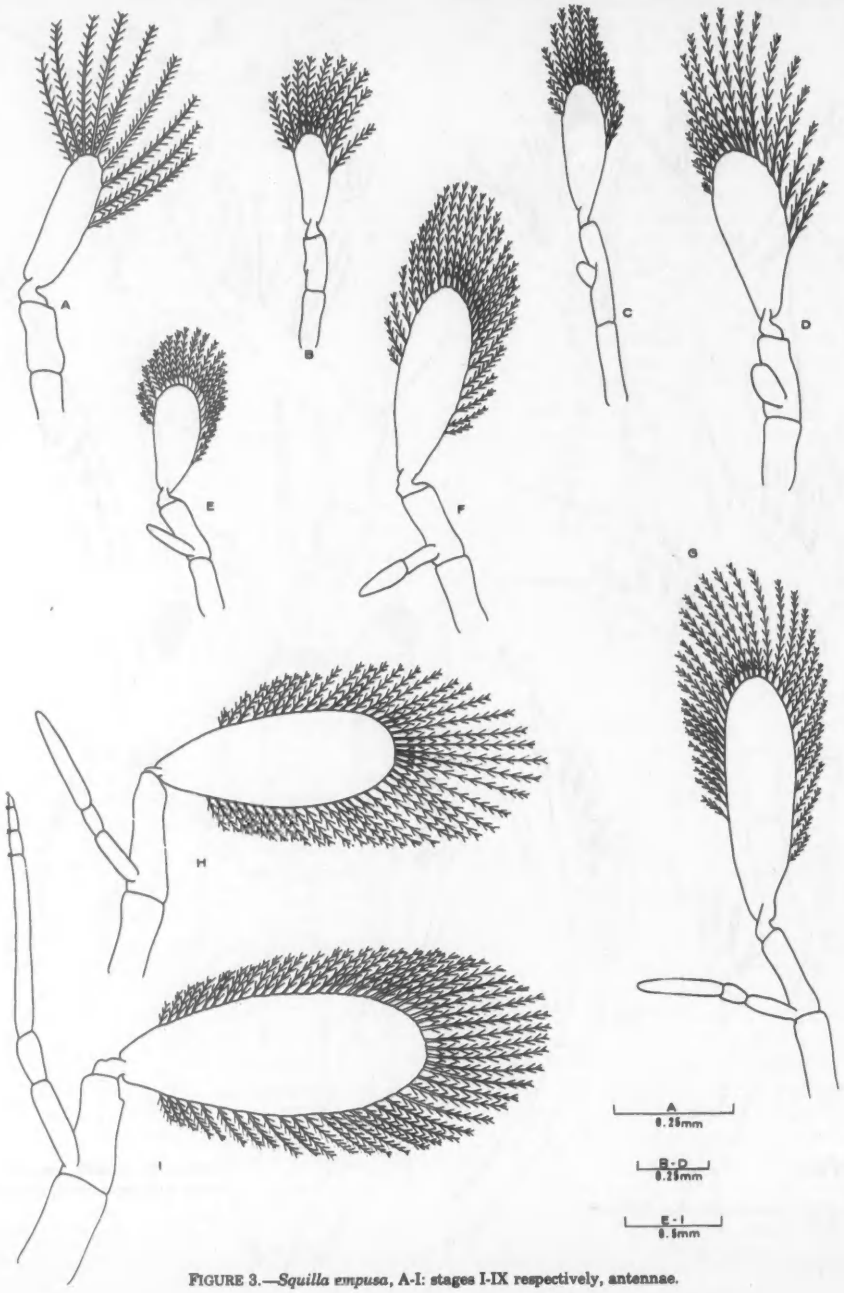


FIGURE 3.—*Squilla empusa*, A-I: stages I-IX respectively, antennae.

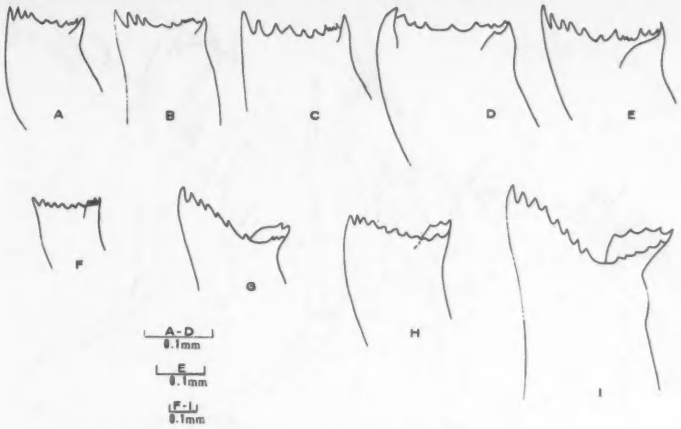
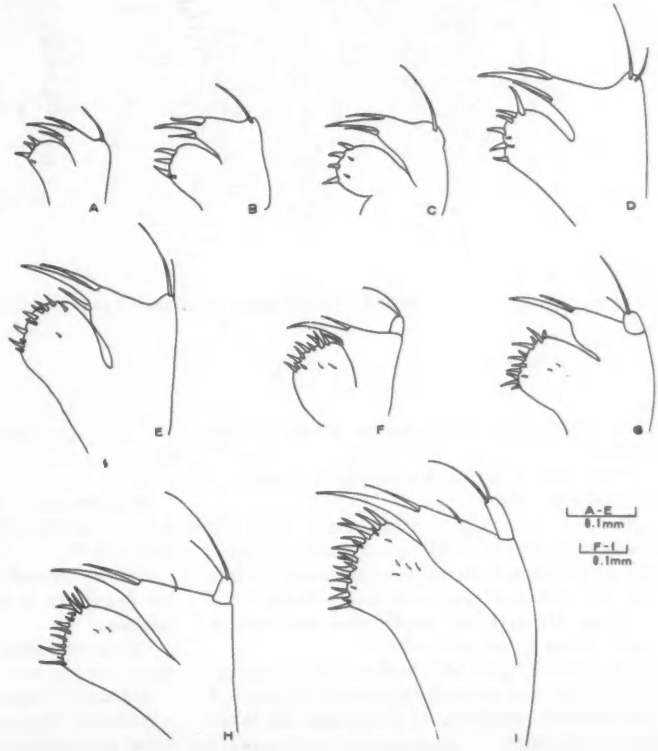


FIGURE 4.—*Squilla empusa*, A-I: stages I-IX respectively, mandibles.

FIGURE 5.—*Squilla empusa*, A-I: stages I-IX respectively, maxillules



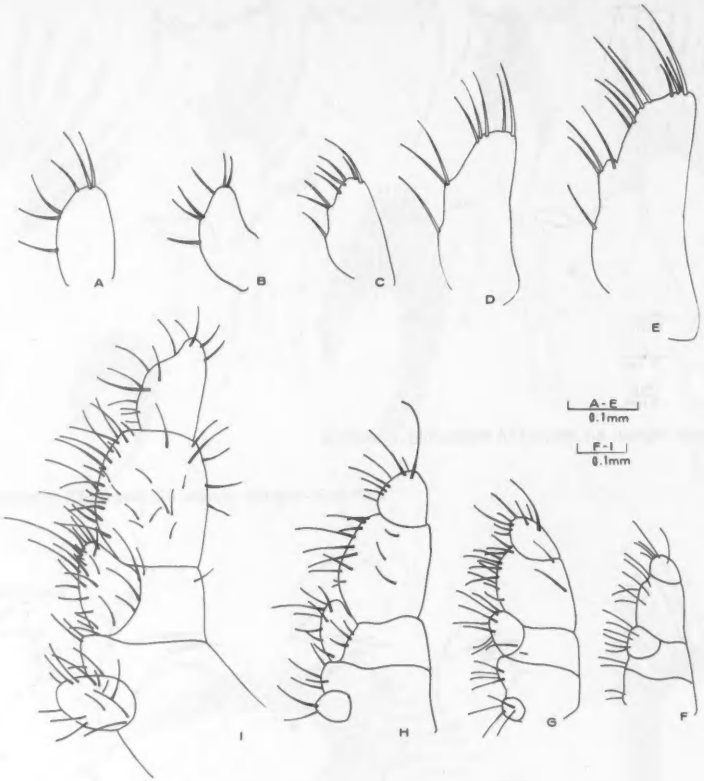


FIGURE 6.—*Squilla empusa*, A-I: stages I-IX respectively, maxillae.

portion of cutting edge minutely serrate. Epipod present.

Third, fourth, and fifth maxillipeds absent.

Pereiopods absent.

Posterolateral angles of pleomeres rounded. Pleopods (Figure 9A to 9D) one through four present with appendix interna. Pleopod setation of this and other larval stages presented in Table 1.

Sixth pleomere not articulated, submedian spines absent, uropods absent.

Pleotelson (Figure 10A) with paired lateral, intermediate, and posterolateral spines, 4 pairs of intermediate denticles, 15 submedian denticles bearing spinules.

Stage II (Figure 1B)

Measurements (mm): RL, 1.35 to 1.55; PL, 0.70 to 0.90; TL, 4.20 to 4.60; CL, 1.05 to 1.30; PW, 0.55 to 0.75.

Rostrum extending well beyond end of antennular flagellum, armed with one to four ventral spinules.

Carapace slightly convex, posterolateral spines extend to anterior section of telson.

Antennule (Figure 2B) as in previous stage.

Antenna (Figure 3B) with 10 to 13 plumose setae, endopod present as incipient bud.

FIGURE 7.—*Squilla empusa*, A-I: stages I-IX respectively, first maxillipeds.

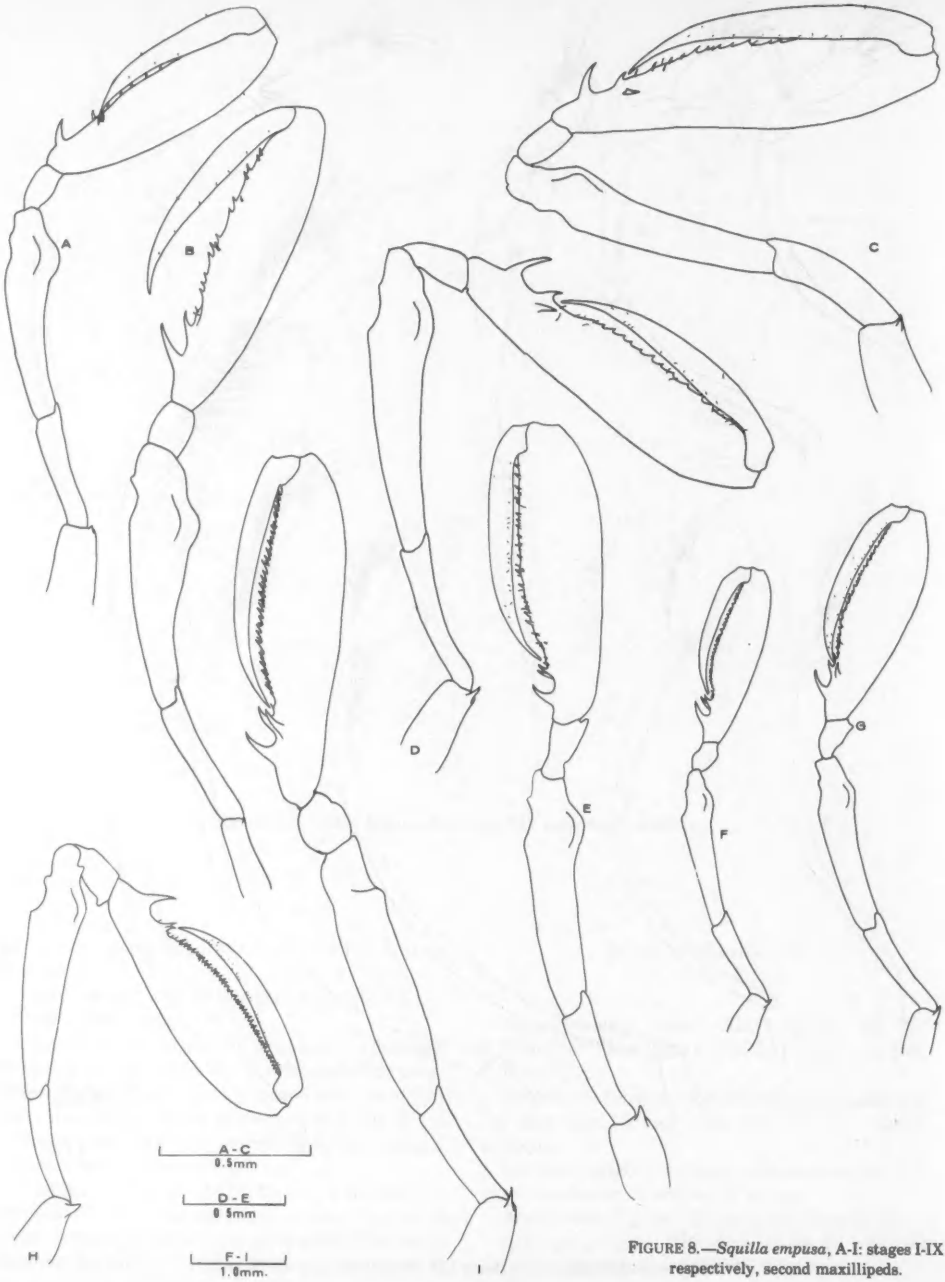


FIGURE 8.—*Squilla empusa*, A-I: stages I-IX respectively, second maxillipeds.

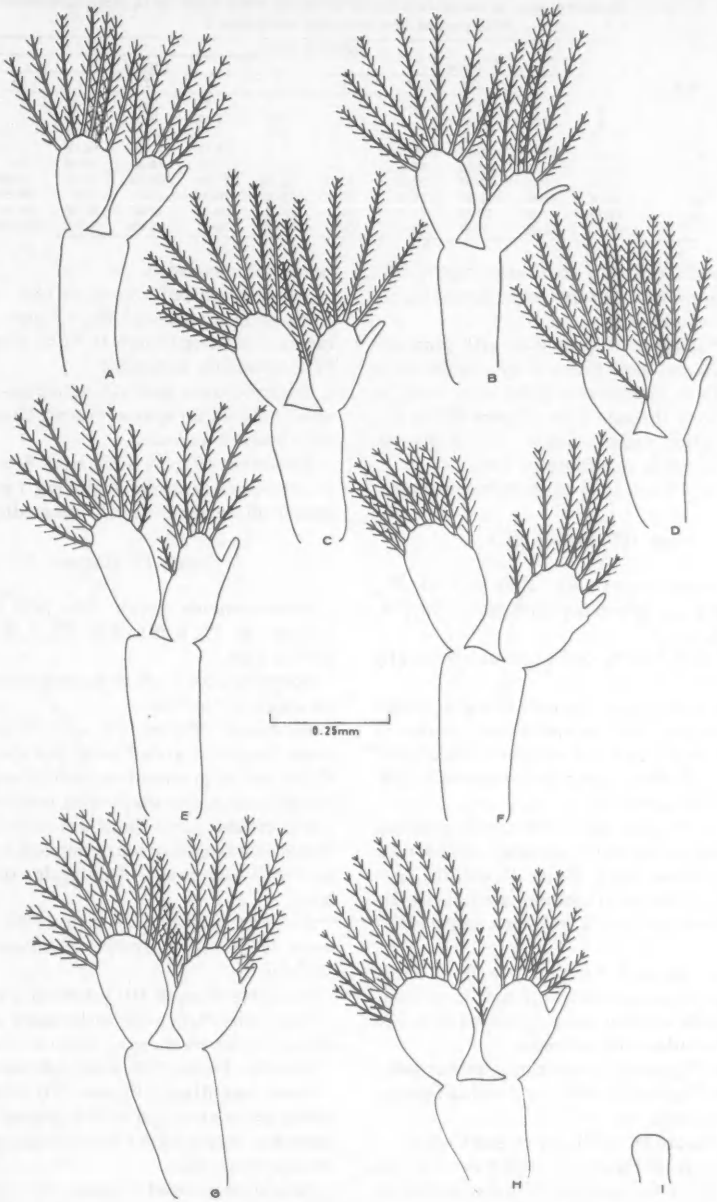


FIGURE 9.—*Squilla empusa*, A-D: stage I, first to fourth pleopods respectively, E-I: stage II, first to fifth pleopods respectively.

TABLE 1.—Number of setae on margins of pleopods for pelagic larval stages I to IX of *Squilla empusa*. Fifth pleopod does not appear until stage V.

	Abdominal somite									
	Endopod					Exopod				
Stage	1	2	3	4	5	1	2	3	4	5
I	6	6	6-7	6-7	—	7	7	7-9	7-9	—
II	6	7-8	7-8	7	—	7-8	9-10	9-11	9-10	—
III	8-10	9-13	10-14	9-14	—	9-10	12-13	13-14	11-14	—
IV	12-13	14-15	15-16	15-17	—	12	16-17	17-18	16-17	—
V	14-15	15-18	16-18	16-20	—	14-15	17-19	19-20	18-19	7-8
VI	16-20	18-25	20-27	20-27	3-8	15-20	21-26	23-29	21-27	12-16
VII	22-28	26-28	26-31	26-32	23-28	22-30	26-31	29-33	28-31	20-23
VIII	25-29	27-32	28-36	31-38	30-39	24-30	32-36	32-38	31-38	24-31
IX	27-31	32-39	35-42	36-45	40-47	36-41	36-41	38-46	37-45	33-39

Mandible (Figure 4B), maxillule (Figure 5B), maxilla (Figure 6B), and first maxilliped (Figure 7B) as in previous stage.

Second maxilliped (Figure 8A) with propodus bearing proximal tooth followed by another large tooth and 19 to 21 denticles along inner margin.

Pleopods one through four (Figure 9E to 9H) increase setation slightly (Table 1). Fifth pleopod (Figure 9I) present as bifurcated bud.

Pleotelson (Figure 10B) as in previous stage.

Stage III (Figure 2C)

Measurements (mm): RL, 1.90 to 2.10; PL, 1.00 to 1.10; TL, 5.80 to 6.50; CL, 1.50 to 1.78; PW, 0.75 to 0.95.

Rostrum with four to eight spinules ventrally for stages III to VIII.

Carapace with lateral margins straight, armed with two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. Posterolateral spines extend to posterior region of pleotelson.

Antennule (Figure 2C) with two-segmented inner flagellum, proximal segment armed with one strong distal seta. Outer flagellum two-segmented with 9 or 10 mesial aesthetascs arranged in three groups of 2 or 3, each group with a weak seta.

Antenna (Figure 3C) with 13 to 16 plumose setae, length of unsegmented endopod increased.

One median ventral spine situated between base of antennules and antennae.

Mandible (Figure 4C) essentially unchanged.

Maxillule (Figure 5C) with coxal endite bearing four to eight teeth.

Macilla (Figure 6C) with six to eight setae.

First maxilliped (Figure 7C) with 9 or 10 strong setae arranged in four groups of 2 or 3 on propodus, carpus with 1 or 2 strong setae distally.

Second maxilliped (Figure 8C) with propodus bearing 23 to 27 denticles, basis with proximal spine well developed.

Third maxilliped present as bud.

Pleopods one through four (Figure 11A to 11D) increase setation (Table 1). Fifth pleopod (Figure 11E) biramous, nonsetose.

Sixth pleomere partially articulated, one pair of small submedian spines present. Uropods (Figure 10C) present as buds.

Pleotelson (Figure 10C) with 8 to 10 pairs of intermediate denticles, including 1 pair in axis of intermediate spines 15 to 27 submedian denticles.

Stage IV (Figure 12)

Measurements (mm): RL, 2.50 to 2.90; PL, 1.20 to 1.40; TL, 6.50 to 6.90; CL, 1.80 to 2.25; PW, 1.00 to 1.20.

Rostrum with a row of minute spinules distally for stages IV to VIII.

Antennule (Figure 2D) with three-segmented inner flagellum armed with two strong setae on distal half of proximal segment. Outer flagellum divided into a two-segmented median flagellum, and a broader outer flagellum with 10 or 11 aesthetascs arranged in four groups of 2 or 3, a small seta with each group. Antennular somite articulated.

Antenna (Figure 3D) with 17 to 19 plumose setae, length of unsegmented endopod increased slightly.

Mandible (Figure 4D) essentially unchanged.

Maxillule (Figure 5D) with coxal endite bearing seven to nine teeth, palp with two setae.

Maxilla (Figure 6D) with eight to nine setae.

First maxilliped (Figure 7D) with 12 or 13 strong setae arranged in five groups of 2 or 3 on propodus, carpus with 4 distal setae, merus with 1 strong distal seta.

Second maxilliped (Figure 8D) with propodus bearing proximal tooth followed by 2 strong teeth in opposition and 25 to 33 denticles along inner margin.

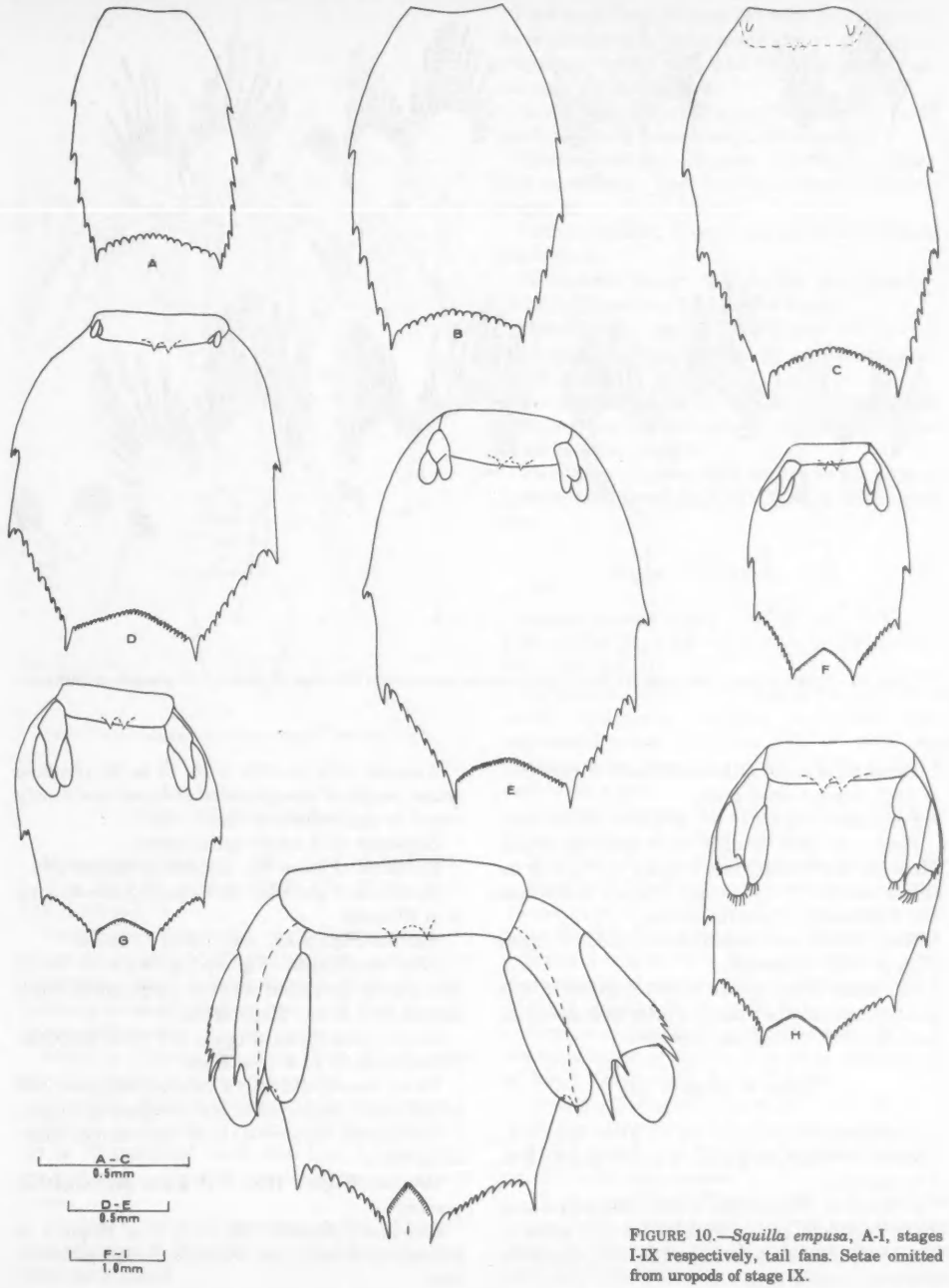


FIGURE 10.—*Squilla empusa*, A-I, stages I-IX respectively, tail fans. Setae omitted from uropods of stage IX.

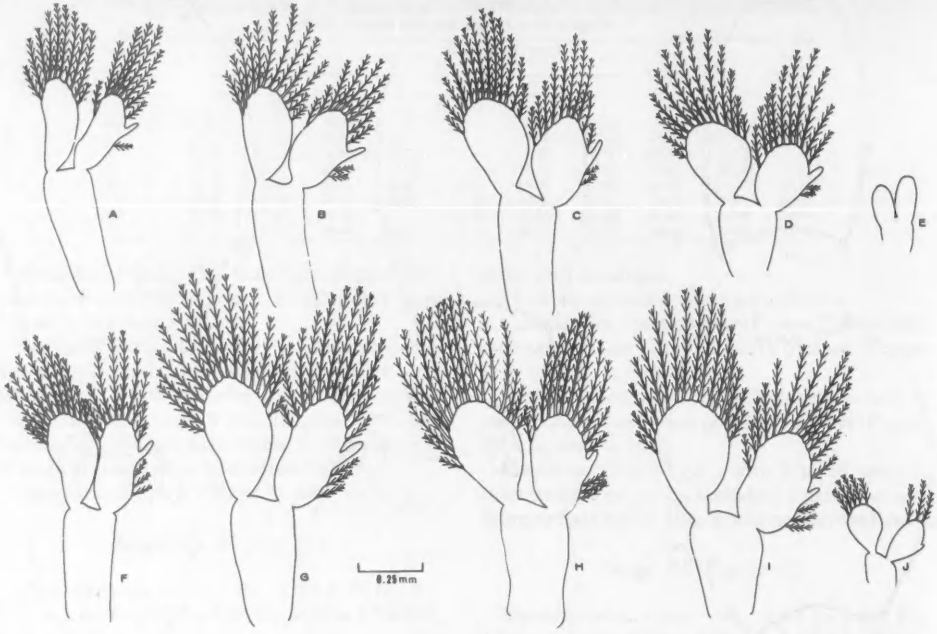


FIGURE 11.—*Squilla empusa*, A-E: stage III, first to fifth pleopods respectively, F-J: stage IV, first to fifth pleopods respectively.

Third, fourth, and fifth maxillipeds (Figure 13A to 13C) unsegmented buds.

Pereiopods (Figure 14A to 14C) present as buds.

Posterolateral angles of pleomeres acute. Pleopods one through four (Figure 11F to 11I) increase setation. Fifth pleopod (Figure 11J) setose and possessing appendix interna.

Sixth abdominal somite articulated. Uropods (Figure 10D) biramous.

Pleotelson (Figure 10D) with 1 denticle in axis of lateral spine, 8 or 9 pairs of intermediate denticles, 23 to 30 submedian denticles.

Stage V (Figure 15)

Measurements (mm): RL, 2.50 to 3.25; PL, 1.50 to 1.65; TL, 8.50 to 9.00; CL, 2.30 to 2.50; PW, 1.40 to 1.60.

Antennule (Figure 2E) with three-segmented inner flagellum armed with two to four setae on distal half of proximal segment; median flagellum also three-segmented.

Antenna (Figure 3E) with 19 to 23 plumose setae, length of unsegmented endopod now nearly equal to segments bearing it.

Epistome with small apical spine.

Mandible (Figure 4E) essentially unchanged.

Maxillule (Figure 5E) with coxal endite bearing 8 to 12 teeth.

Maxilla (Figure 6E) with 10 or 11 setae.

First maxilliped (Figure 7E) with 13 to 17 strong setae arranged in five or six groups of 2 to 4, carpus with 5 to 8 distal setae.

Second maxilliped (Figure 8E) with propodus armed with 30 to 43 denticles.

Third, fourth, and fifth maxillipeds (Figure 13D to 13F) still unsegmented, but increased in length.

Pereiopods (Figure 14D to 14F) present as bifurcated buds.

Uropods (Figure 10E) with basal prolongation present.

Pleotelson (Figure 10E) with 8 to 10 pairs of intermediate denticles, 28 to 33 submedian denticles.

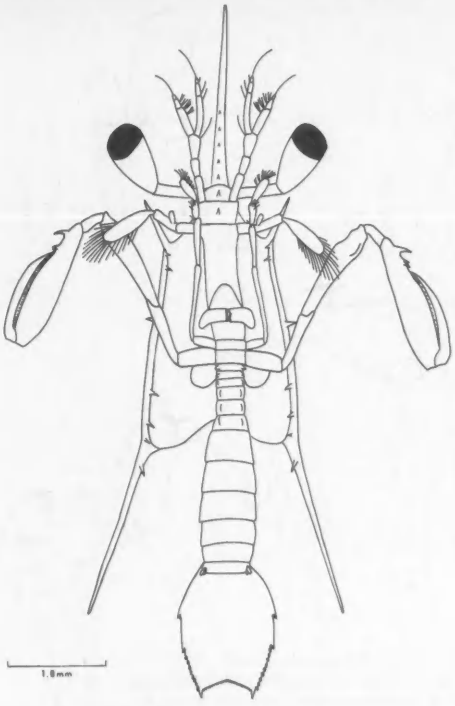


FIGURE 12.—*Squilla empusa*, stage IV, ventral view.

Stage VI (Figure 17A)

Measurements (mm): RL, 3.00 to 3.50; PL, 1.65 to 2.00; TL, 9.80 to 10.60; CL, 2.65 to 2.95; PW, 1.45 to 1.75.

Antennule (Figure 2F) with four-segmented inner flagellum. Median flagellum with three segments. Outer flagellum with 12 to 14 aesthetascs arranged in four groups of 2 or 3, each group with a seta.

Antenna (Figure 3F) with 22 to 25 plumose setae, endopod now two-segmented.

Mandible (Figure 4F) essentially unchanged.

Maxillule (Figure 5F) with coxal endite bearing 10 to 12 marginal teeth and 1 or 2 very short medial setae, palp well developed, armed with 2 setae.

Maxilla (Figure 6F) five-segmented, subproximal segment with endite bearing 14 to 19 setae. Palp articulated.

First maxilliped (Figure 7F) with 18 to 22 strong setae arranged in six or seven groups of 2 to 4 on propodus, carpus with 8 to 12 distal setae, conspicuous epipod present.

Second maxilliped (Figure 8F) with 33 to 47 denticles along inner margin of propodus.

Third maxilliped (Figure 13G) with endopod four-segmented, dactylus not reflected against propodus.

Fifth maxilliped (Figure 13I) with endopod unsegmented.

Pereiopods (Figure 14G to 15I) unsegmented, distally bifurcate, increased in length.

Pleopods one through five (Figure 16F to 16J) with gills present as buds on inner proximal margin of exopod.

Uropods (Figure 10F) with basal prolongation half length of endopod, exopod with or without one spine on outer margin.

Pleotelson (Figure 10F) with 8 to 10 pairs of intermediate denticles. 29 to 33 submedian denticles.

Stage VII (Figure 17B)

Measurements (mm): RL, 3.20 to 3.70; PL, 2.00 to 2.20; TL, 11.60 to 13.60; CL, 2.85 to 3.55; PW, 1.85 to 2.30.

Antennule (Figure 2G) with seven-segmented inner flagellum, median flagellum five-segmented, outer flagellum with 18 or 19 aesthetascs arranged in five or six groups of 2 or 3, each with a seta.

Antenna (Figure 3G) with 32 to 39 plumose setae, endopod with three segments.

Mandible (Figure 4G) essentially unchanged.

Maxillule (Figure 5G) with coxal endite bearing 13 marginal teeth and 2 medial setae, endite with spine flanked by 1 strong seta. Palp unchanged.

Maxilla (Figure 6G) four-segmented, the two more proximal segments each with one endite. Maxilla armed with 32 to 34 setae.

First maxilliped (Figure 7G) with 23 to 26 strong setae on propodus, in seven or eight groups of 2 to 4, carpus with 21 to 27 setae.

Second maxilliped (Figure 8G) with 52 to 60 denticles along inner margin of propodus.

Third, fourth, and fifth maxillipeds (Figure 13J to 13L) fully articulated.

Third maxilliped (Figure 13J) with dactylus armed with spinules and reflected against propodus, latter armed with 10 or 11 spinules, carpus with 4 to 6 spinules.

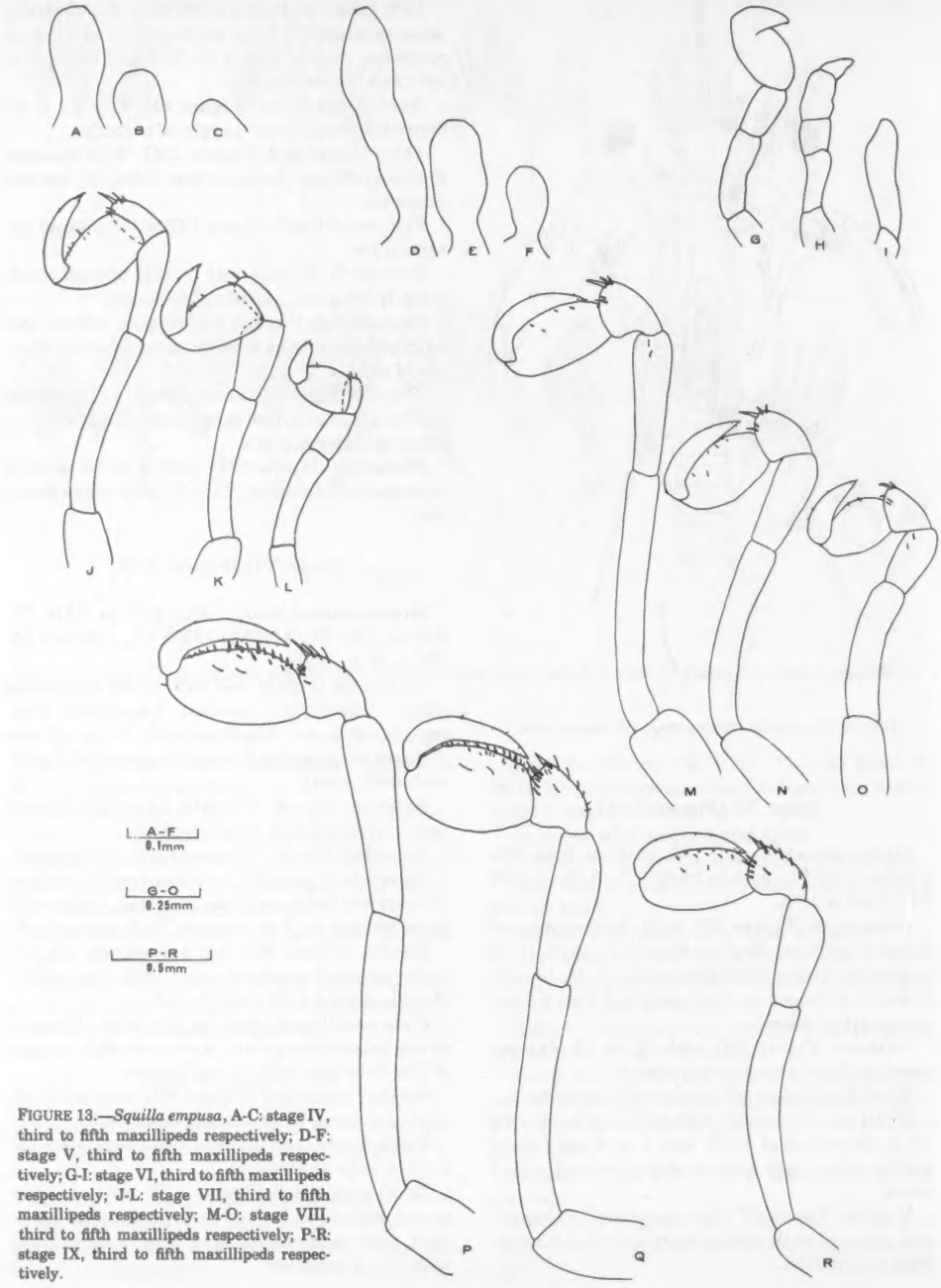


FIGURE 13.—*Squilla empusa*, A-C: stage IV, third to fifth maxillipeds respectively; D-F: stage V, third to fifth maxillipeds respectively; G-I: stage VI, third to fifth maxillipeds respectively; J-L: stage VII, third to fifth maxillipeds respectively; M-O: stage VIII, third to fifth maxillipeds respectively; P-R: stage IX, third to fifth maxillipeds respectively.

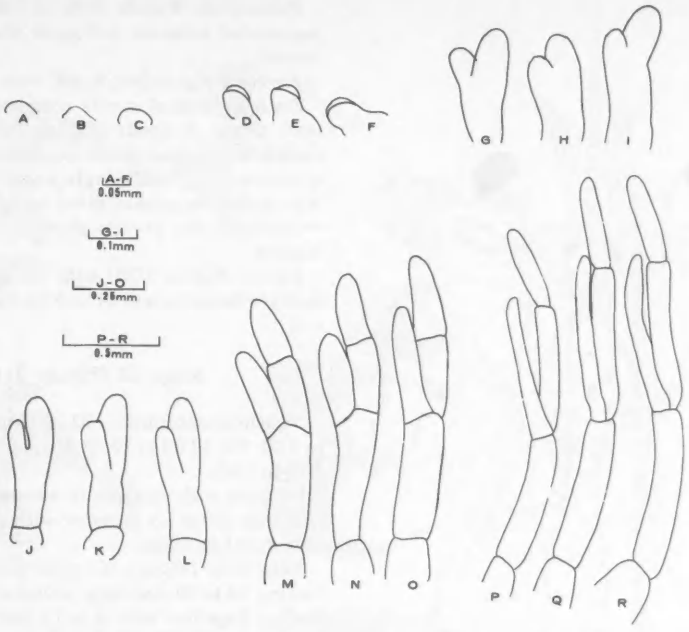


FIGURE 14.—*Squilla empusa*, A-C: stage IV, first to third pereiopods respectively; D-F: stage V, first to third pereiopods respectively; G-I: stage VI, first to third pereiopods respectively; J-L: stage VII, first to third pereiopods respectively; M-O: stage VIII, first to third pereiopods respectively; P-R: stage IX, first to third pereiopods respectively.

Fourth maxilliped (Figure 13K) with dactylus armed with spinules and partially reflected against propodus, latter armed with four to eight spinules, carpus with four to six spinules, epipod present.

Fifth maxilliped (Figure 13L) segmented, dactylus unarmed and not reflected against unarmed propodus, carpus with zero to three spinules.

Pereiopods (Figure 14J to 14L) with clearly differentiated endopods and exopods, though segmentation not yet distinct.

Pleopods (Figure 18A to 18E) with bilobed rudimentary gills.

Sixth pleomere partially separated from telson. Uropods (Figure 10G) with basal prolongation acute. Exopod with one or two spines on outer margin, armed with zero to five plumose setae. Endopod with zero to two plumose setae.

Pleotelson (Figure 10G) with 9 or 10 pairs of intermediate denticles, 32 to 35 submedian denticles.

Stage VIII (Figure 19)

Measurements (mm): RL, 3.25 to 3.45; tL, 2.30 to 2.50; TL, 13.90 to 15.30; CL, 3.90 to 4.35; TW, 2.25 to 2.65.

Antennule (Figure 2H) with inner flagellum bearing 9 to 11 distinctly articulated segments. Median flagellum with five to seven distinct segments. Outer flagellum with 21 to 23 aesthetascs arranged in six or seven groups of 2 or 3, each group with a seta in addition.

Antenna (Figure 3H) with 40 to 55 plumose seta.

Mandible (Figure 4H) essentially unchanged.

Maxillule (Figure 5H) with coxal endite bearing 15 to 19 marginal teeth and 2 to 4 medial setae, distal margin of basis with 1 median seta.

Maxilla (Figure 6H) armed with 40 to 58 setae.

First maxilliped (Figure 7H) with 29 to 31 strong setae on propodus arranged in eight groups of 2 to 5, carpus with 37 to 44 setae.

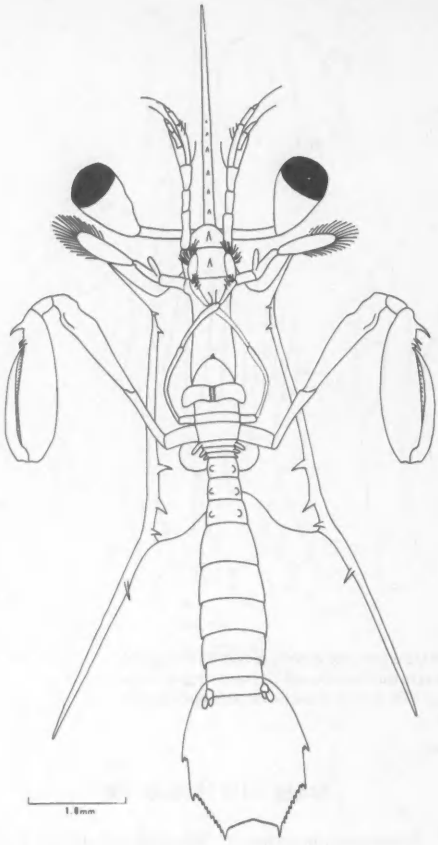


FIGURE 15.—*Squilla empusa*, stage V, ventral view.

Second maxilliped (Figure 8H) with 61 to 75 denticles on propodus.

Third, fourth, and fifth maxillipeds (Figure 13M to 13O) with dactylus armed with spinules and reflected against propodus, epipods present.

Third maxilliped (Figure 13M) with propodus armed with 12 to 21 spinules, carpus with 6 to 9 spinules.

Fourth maxilliped (Figure 13N) with propodus armed with 12 to 16 spinules, carpus with 5 to 8 spinules.

Fifth maxilliped (Figure 13O) with propodus armed with 6 to 11 spinules, carpus with 4 to 7 spinules.

Pereiopods (Figure 14M to 14O) with two-segmented exopods, endopods shorter, unsegmented.

Pleopods (Figure 20A to 20E) with trilobed gills.

Sixth abdominal somite completely separated from telson. Uropods (Figure 10H) with two-segmented exopod. Basal segment with 2 to 4 spines on outer distal margin, apical segment with 4 to 14 plumose setae on distal margin. Endopod of uropod with four to eight plumose setae on distal margin.

Telson (Figure 10H) with 10 pairs of intermediate denticles and 31 to 35 submedian denticles.

Stage IX (Figure 21)

Measurements (mm): RL, 2.40 to 4.50; tL, 2.30 to 2.60; TL, 13.00 to 17.50; CL, 3.00 to 3.90; TW, 2.10 to 2.80.

Rostrum with decrease in number of spinules, now with two to six spinules; with or without minute distal spinules.

Antennule (Figure 2I) with inner flagellum bearing 14 to 20 distinctly articulated segments. Median flagellum with 8 to 11 distinctly articulated segments. Outer flagellum with 23 to 33 aesthetascs arranged in seven to nine groups of 2 to 7, each group with a seta.

Antenna (Figure 3I) with 48 to 60 plumose setae, endopod with 6 to 9 segments.

Mandible (Figure 4I) essentially unchanged.

Maxillule (Figure 5I) with coxal endite bearing 20 to 25 marginal teeth and 1 or 2 medial setae, margin of basal endite with 1 or 2 setae.

Maxilla (Figure 6U) with 78 to 131 setae.

First maxilliped (Figure 7I) with 35 to 44 setae arranged in 9 or 10 groups of 2 to 5, carpus with 59 to 107 setae, dactylus with or without cluster of setae on median outer margin, propodus with or without cluster of setae on distal outer margin.

Second maxilliped (Figure 8I) with 71 to 92 denticles on propodus.

Dactylus of third, fourth, and fifth maxillipeds (Figure 13P to 13R) with or without regularly spaced setae along outer margin, propodus with or without a cluster of setae on distal outer margin.

Third maxilliped (Figure 13P) with propodus bearing 19 to 56 spinules, carpus with 11 to 22 spinules.

Fourth maxilliped (Figure 13Q) with propodus bearing 17 to 51 spinules, carpus with 10 to 28 spinules.

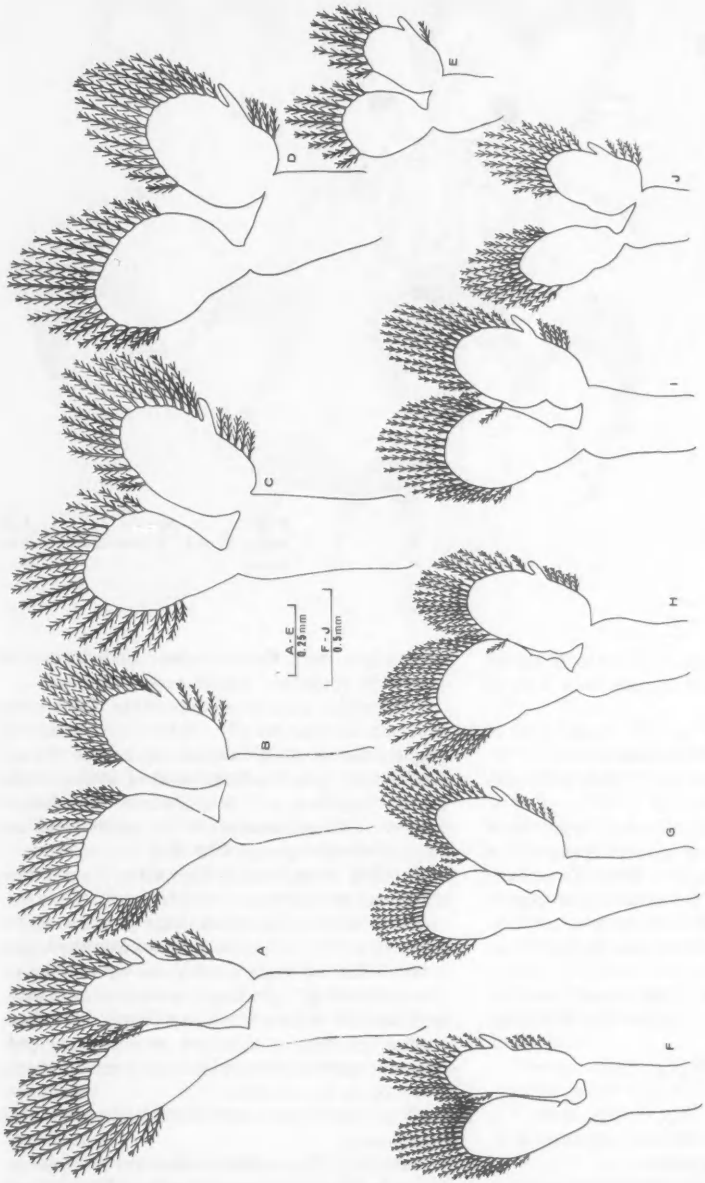


FIGURE 16.—*Squilla empusa*, A-E: stage V, first to fifth pleopods respectively; F-J: stage VI: first to fifth pleopods respectively.

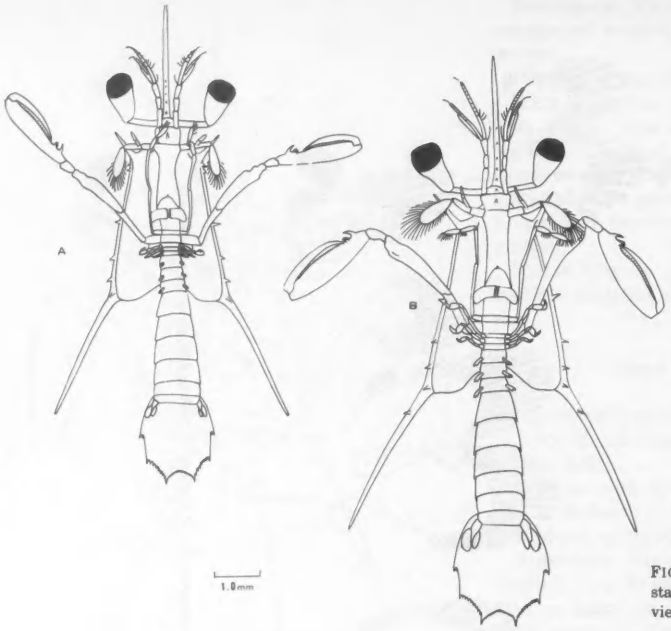


FIGURE 17.—*Squilla empusa*, A-B: stages VI and VII respectively, ventral views.

Fifth maxilliped (Figure 13R) with propodus bearing 18 to 40 spinules, carpus with 9 to 20 spinules.

Pereiopods (Figure 14P to 14R) slender with or without distal segment of exopods setose.

Pleopods (Figures 22A to 22C; 23A, 23B) with distal lobe of gill pinnate.

Uropod (Figure 26C) with basal segment of exopod armed with 6 to 8 spines, apical segment of exopod with 17 to 60 plumose setae. Endopod of uropod with 10 to 38 plumose setae. Inner spine of basal prolongation with blunt spine on outer proximal margin. Basal uropod segment with a dorsal spine on distal margin.

Telson (Figure 14I) with 8 to 10 pairs of intermediate denticles, 26 to 34 submedian denticles.

Postlarva (Figure 24)

Measurements (mm): RL, 0.50 to 0.60; CL, 2.90 to 3.30; TW, 2.55 to 3.10; RW, 0.65 to 0.75; tL, 1.95 to 2.55; TL, 12.3 to 14.20.

Eyes large, extending to middle of second segment of antennular peduncle. Cornea bilobed, set obliquely on stalk. Ocular scales rounded, anterior margin of opthalmic somite evenly rounded.

Antennular process produced into blunt spine directed anterolaterally, antennular peduncle slightly shorter than carapace, antennule (Figure 25A) with inner flagellum bearing 34 segments, median flagellum with 30 segments, outer flagellum with 15 segments and 22 aesthetascs arranged in eight groups of 2 or 3.

Antenna (Figure 25B) with 63 to 75 plumose setae, endopod with 16 segments.

Rostral plate wider than long, lateral margins tapering to rounded apex. Median carina present.

Anterolateral angle of carapace without spine, almost forming right angle, posterolateral margins broadly rounded, carinae poorly developed, median carina not bifurcate anteriorly or posteriorly, intermediate and lateral carinae present, reflected carinae absent.

Mandible (Figure 25C) serrate, mandibular palp absent.

Maxillule (Figure 25D) with coxal endite bearing 26 to 27 strong marginal teeth and 6 to 9 small medial teeth. Basal endite with one spine flanked

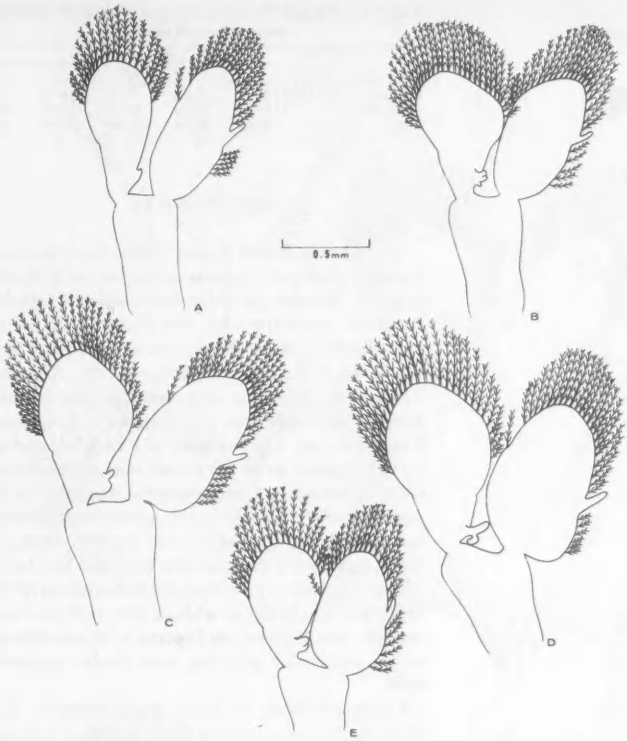


FIGURE 18.—*Squilla empusa*, A-E: stage VII, first to fifth pleopods respectively.

by one strong seta. Distal margin of basis with three setae. Endopod present as palp on distal margin of basis, armed with two setae.

Maxilla (Figure 25E) four-segmented, two proximal segments with endites, second bilobed.

Five pairs of maxillipeds (Figure 25F to 25J) each maxilliped with one epipod. First maxilliped (Figure 25F) with distal margin of propodus bearing 14 teeth, inner margin with 48 to 50 strong setae arranged in 10 transverse rows, 2 or 3 most distal setae spatulate with strong setules.

Second maxilliped (Figure 25G) with dactylus bearing six teeth, pectinate propodus with three moveable proximal spines, dorsal ridge of carpus undivided.

Pereiopods (Figure 26A) with setose endopod and exopod.

Last three thoracic somites with unarmed submedian and intermediate carinae. Lateral process of fifth thoracic somite subacute, sloping posteriorly. Lateral processes of next two somites bilobed each with a small anterior lobe and a large broadly rounded posterior lobe. Median ventral keel of eighth somite with rounded apex.

Abdomen broad, depressed, Submedian, intermediate, lateral, and marginal carinae present. Abdominal spines in submedian carinae of sixth somite, intermediate and lateral carinae of fifth and sixth somites, and marginal carinae of fifth somite, formula: submedian 6; intermediate 5 to 6; lateral, 5 to 6; marginal, 5. Sixth abdominal somite with sharp ventral spine anterior to uropod articulation.

Pleopods (Figure 26B to 26F) with gills. Pleopod setation presented in Table 2.

Uropod (Figure 26G) with eight graded moveable spines on outer margin of proximal segment of exopod, last extending to middle of apical segment. Apical segment of exopod extending posteriorly to apex of intermediate spine. Basal seg-

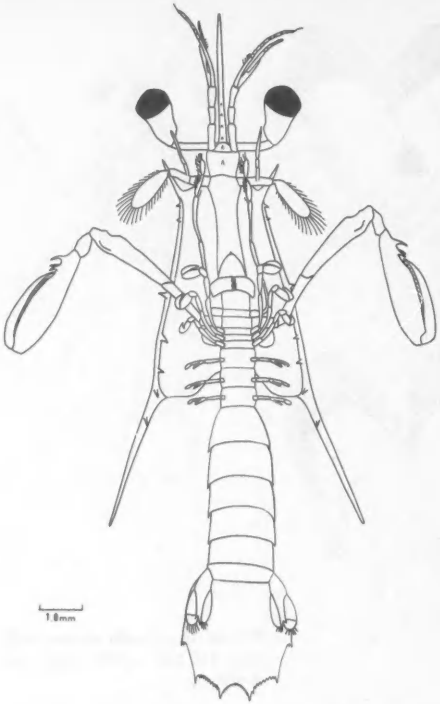


FIGURE 19.—*Squilla empusa*, stage VIII, ventral view.

ment of uropod with dorsal spine on distal margin. Basal prolongation of uropod with two spines, mesial longer. Single rounded lobe between spines of prolongation. Mesial margin of basal prolongation sinuate.

Telson (Figure 24) as wide as long, median carina with sharp posterior spine, prelateral lobes absent, postanal ventral carina absent, submedian teeth with moveable apices, denticle formula: submedian, 8 to 10; intermediate, 7 to 10; lateral, 1.

Postlarva white with brown chromatophores on eyes and all appendages except mouthparts. Carapace with few chromatophores. Exposed thoracomeres with chromatophores along posterior margin. Pleomeres with chromatophores along intermediate and lateral carinae and posterior margin. Telson with chromatophores along curved dorsal striations and posterior spine.

TABLE 2.—Number of setae on margins of pleopods of the postlarva of *Squilla empusa*.

Structure	Abdominal somite				
	1	2	3	4	5
Protopod	12-15	12-15	12-15	12-14	8-11
Endopod	55-60	60-71	65-72	63-72	59-67
Exopod	55-59	61-64	62-64	61-63	53-56

DISCUSSION

Brooks (1878) and Faxon (1882) have produced the only prior publications on the larvae of *Squilla empusa*. Brooks partially described the development by reconstruction, and Faxon held an unidentified last stage through metamorphosis to attempt to identify it with the adult. Although Brooks' illustrations and descriptions indicate that he probably was working with *S. empusa*, Faxon's do not. The carapace of Faxon's last stage larvae appears to be too broad, the posterolateral spines are too short, and a spinule is present on the posterior margin of the carapace midway between the dorsal and posterolateral spines. Furthermore, in Faxon's illustrations both the last larval stage and postlarva have broad abdomens with the first pleomere being as wide as the sixth, but in *S. empusa*, the abdomen is tapered with smaller anterior pleomeres grading into larger posterior ones.

Faxon collected his larva from Newport, R.I., where only four species of stomatopods are known to reside: *S. empusa, Nannosquilla grayi, Heterosquilla armata*, and *Platysquilla enodis* (Manning 1974). Because the telson of Faxon's postlarva bears four intermediate denticles, it can be attributed to the Squillidae, and *S. empusa* is the only squillid known to inhabit the area; the other three species belong to the Lysiosquillidae. Few larval descriptions have been made on southern species of squillid larvae, and of these none possesses the pair of spines on the posterior margin of the carapace, seen in Faxon's larva, nor does *S. empusa*. If Alikunhi (1952, 1967) was correct in his identification of the late larva and postlarva, these spines occur on *Cloridopsis scorpio* from the Indian Ocean. The spines may be only a specific character or they may be diagnostic for the genus *Cloridopsis*. The only member of that genus inhabiting the waters of the Western Atlantic is *C. dubia* which ranges from South Carolina to Brazil. Perhaps Faxon collected a larva of *C. dubia* which drifted north with the Gulf Stream. Until more larval descriptions are worked out for western At-

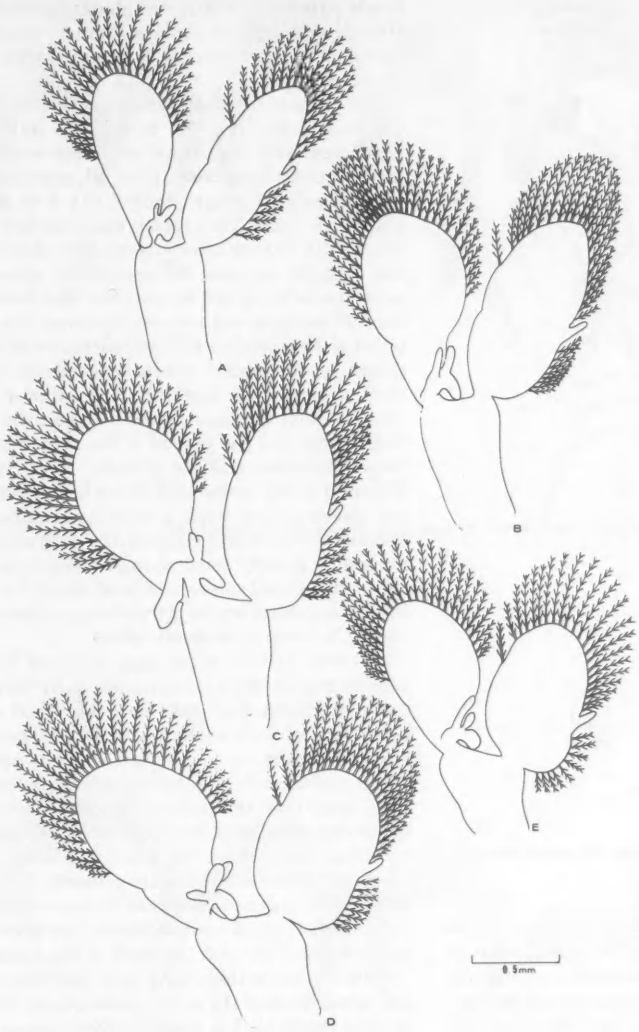


FIGURE 20.—*Squilla empusa*, A-E: stage VIII, first to fifth pleopods respectively.

lantic species of stomatopods, the identity of Faxon's larva will remain uncertain.

To identify larvae of *S. empusa* the spinules of the carapace and denticles of the telson should be examined. Stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles. The third to ninth stages are armed with six spinules on the lateral margin of the carapace. There are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. The telsons of stages III to IX have 8 to 10 intermediate denticles.

Except for Provenzano and Manning (1978), who reared *Gonadactylus oerstedii* from hatching to metamorphosis, experimenters who have at-

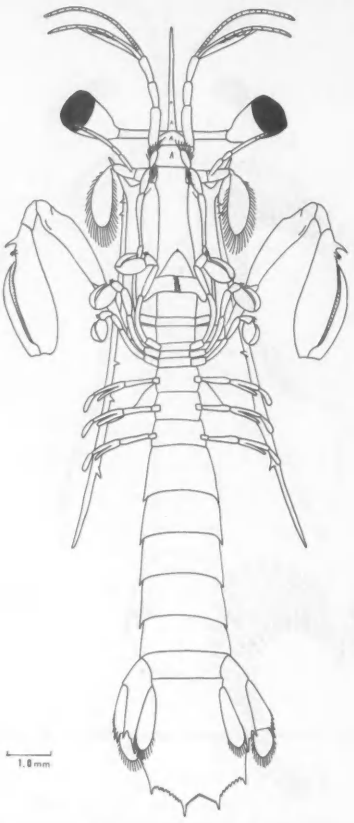


FIGURE 21.—*Squilla empusa*, stage IX, ventral view.

tempted to hatch and rear larvae either to link them with an adult or to describe the entire larval development have been unsuccessful at rearing larvae past the first pelagic stage because the larvae could not be induced to feed (Manning and Provenzano 1963). Pyne (1972) was unable to rear *Pterygosquilla armata schizodontia* eggs past the first pelagic stage, but did hold stages I to VII larvae taken from the plankton for periods as long as 10 to 16 days wherein the larvae passed through at least one ecdysis. Pyne also found it possible to keep later stage larvae for very much longer periods of up to 165 days during which time they molted as many as six times. Pyne reared his larvae in mass culture using 4-in (10.2-cm) finger bowls. Alikunhi (1975) reared planktonic larvae of *Oratosquilla nepa* in aquaria through metamorphosis until they reached adulthood, bred, and produced eggs.

The manner in which all species of Squillidae develop is similar. All Squillidae hatch as pseudozoeae with four pairs of pleopods and develop into the alima form. Some, if not all, pass through two propelagic stages before the first truly planktonic stage. The alima is characterized by a telson with four or more intermediate denticles, the distance between the submedian spines in later stages being not larger than that between the intermediate and submedian spines, the propodus of the second maxilliped bearing three basal spines, the antennular somite generally having a median spine, the posterolateral spine of the carapace having a basal accessory spine, the eyestalks long, and the exopod of the uropod being longer than the endopod (Gurney 1942, 1946). Alikunhi (1952) added that alima larvae possess carapaces armed with a varying number of spinules on the lateral margins, the sixth abdominal somite usually being equipped with a pair of submedian dorsal spines, and in advanced larvae, the posterolateral angles of the abdominal somites ending in acute or subacute spines.

Alikunhi (1952) noted that between allied species, the specific differences are often "trivial" but remarkably constant. He determined that some features, such as the size of the final pelagic stage, the shape and spinulation of the carapace, telson, and uropods, and the presence or absence of teeth other than the terminal on the dactylus of the second maxilliped, hardly show any variation within a species. These characters may be used for specific determinations but are presently of little aid in defining generic alliances for three reasons.

First, relatively few stomatopods have been associated definitely with the adult of the species.

Second, most of these have had described only one larval stage of the entire development. Only 19 of the Squillidae have been definitely connected with their larval forms. Provenzano and Manning (1978) listed 17 species of identified stomatopod larvae, but *O. massavensis* was omitted and *S. empusa* has now been added to the list. Of the 19 species, only 2, *P. armata schizodentia* and *S. empusa*, have been reared in the laboratory through essentially their entire pelagic development. Two additional species have been hatched from eggs obtained from a known adult and the first pelagic stage described, i.e., *Clorida choprai* by Gurney

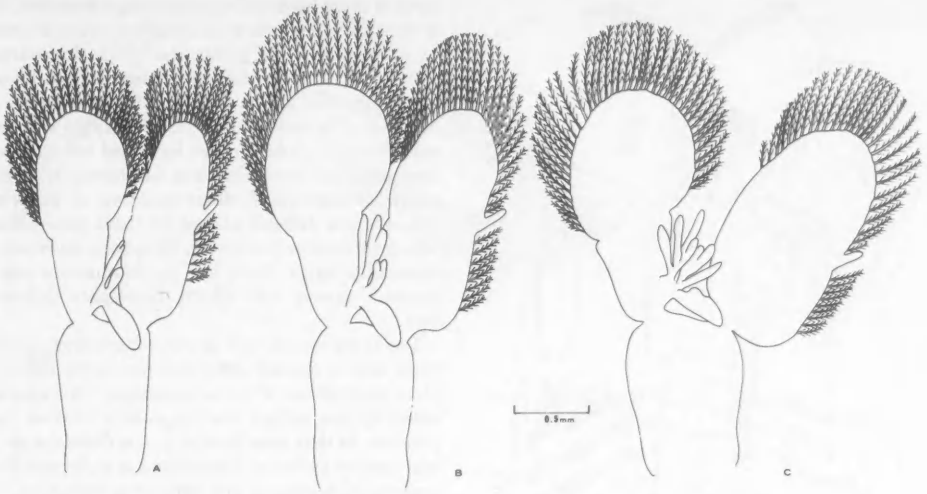


FIGURE 22.—*Squilla empusa*, A-C: stage IX, first to third pleopods respectively.

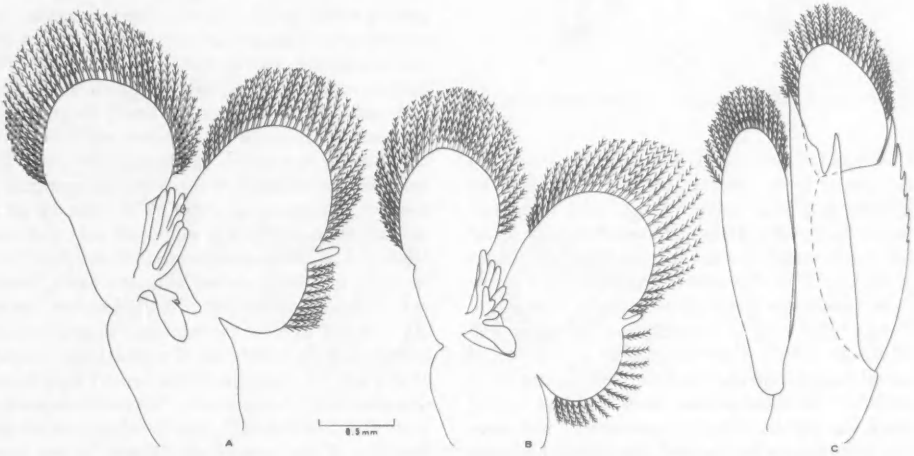


FIGURE 23.—*Squilla empusa*, A-B: stage IX, fourth to fifth pleopods respectively; C: stage IX, uropod.

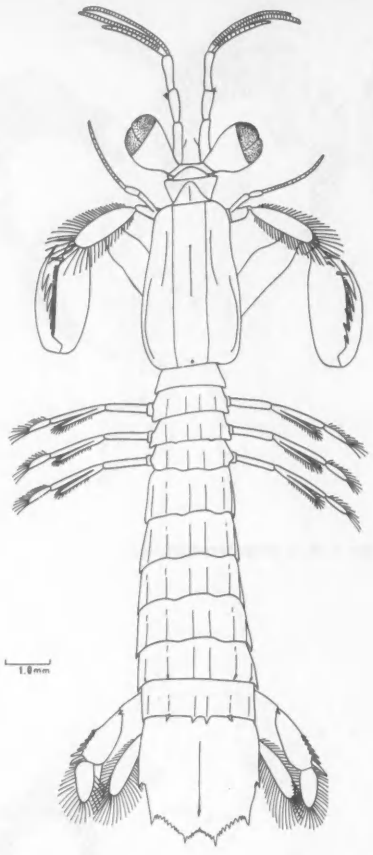


FIGURE 24.—*Squilla empusa*, postlarva, dorsal view.

(1946) and *S. mantis* by Giesbrecht (1910), and the remainder have had the last stage described by holding the final pelagic stage until metamorphosis occurred and the stomatopod could be correlated with an adult of the species. Reconstructions of the larval development of three species, *S. mantis* by Giesbrecht (1910), *O. oratoria* by Komai and Tung (1929), and *O. massavensis* by Gohar and Al-Kholy (1957), were attempted by collecting larval stages from the plankton and piecing them together. Metamorphosis from the last larval stage was obtained for *O. massavensis*, but since the larvae were not reared, the larval histories may not be entirely factual. Thus, because so few larval forms have been identified and because most of these have had only one stage described, it is difficult to discover which characters are shared by all members of a genus and which characters are only specific. Of the nine genera of Squillidae which have had larvae described, four genera have had one or more larval stages of a single species described, four more genera have had two species identified, and one genus has had larvae of eight species described. A determination of generic characters is difficult at best for those genera for which only one or two species have been described, especially since there are no adequately represented genera with which to compare characters.

The third reason why specific characters are of little help in generic definition lies in the incomplete descriptions of the larval stages. Characters noted by one author are frequently omitted by another, so that even for the genus *Oratosquilla*, represented by larval descriptions of eight species, consistent characters are difficult to recognize.

An assessment of larval characters was attempted to determine which ones were constant within each genus. Most characters mentioned in the descriptions appeared to vary a great deal for the species within a genus, or the characters that varied relatively little within a genus were frequently found in other species of different genera. Of possible value in defining generic associations is the presence or absence of teeth (other than the terminal) on the dactylus of the second maxilliped. These teeth occur during the last stage in the genera *Anchisquilla*, *Clorida*, *Pterygosquilla*, and *Squilloides*, although for each of these genera larvae of only one species have been described. The dactylus of *P. armata schizodontia* is armed with 5 to 8 teeth and the first stage is easily diagnosed by the posterior spines of the carapace which bear 6 to 16 spirally arranged, proximal spinules. The spinules are replaced by three ventral spinules in the remaining stages (Pyne 1972). The dactyl of the second maxilliped is equipped with two free teeth in *A. fasciata*, three teeth in *S. lata*, and in *C. latreillei* is usually armed with one tooth, rarely with two (Alikunhi 1952). Newly hatched larvae of *C. choprai* were too inadequately described to be compared with *C. latreillei* (Tweedie 1935; Gurney 1946), but the dactylus of the second maxilliped was observed to be unarmed. This is not surprising since *C. latreillei* and *S. lata* develop teeth on the dactylus of the second maxilliped in the later stages and *P. armata schizodontia* develops its first tooth in the third stage.

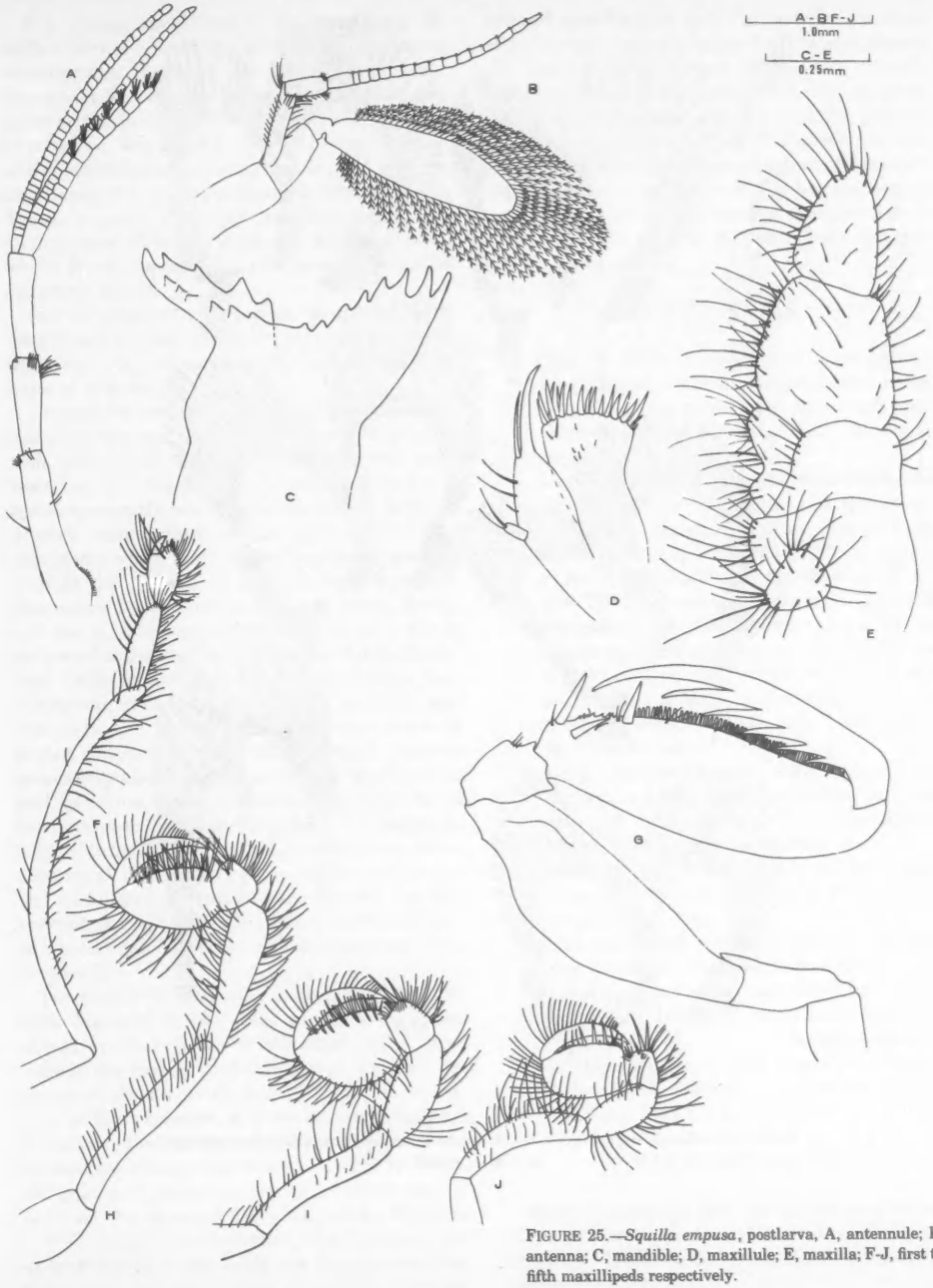


FIGURE 25.—*Squilla empusa*, postlarva, A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F-J, first to fifth maxillipeds respectively.

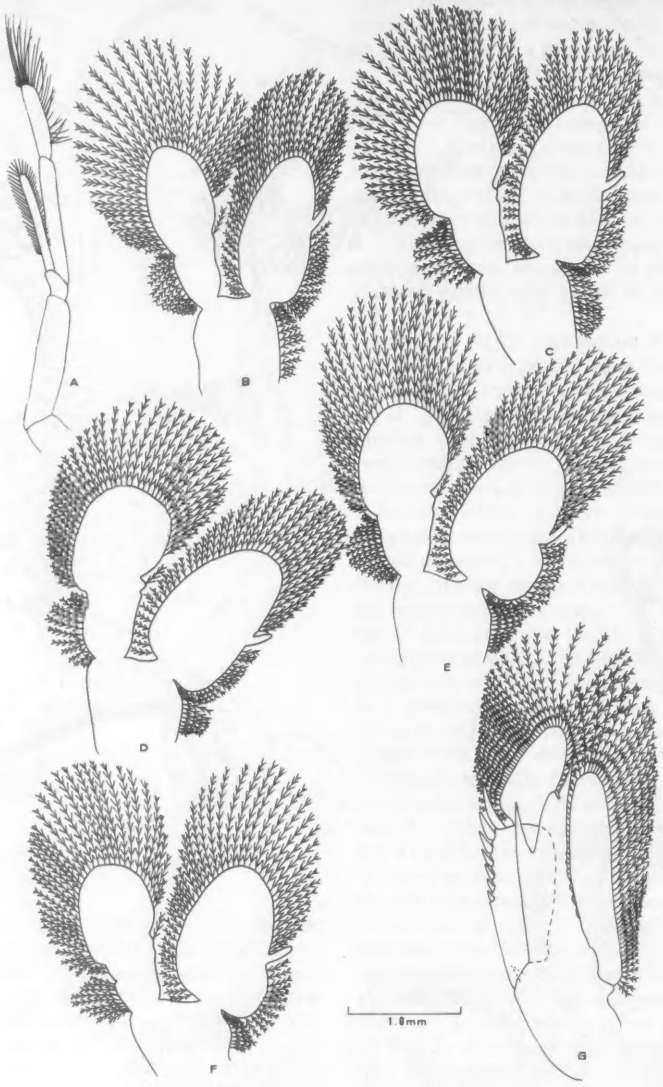


FIGURE 26.—*Squilla empusa*, postlarva, A, first pereipod; B-F, first to fifth pleopods respectively; G, uropod.

The second maxilliped of the remaining described larvae is unarmed throughout the larval development. To distinguish these genera, other characters, such as the presence or absence of a spine on the basis of the second maxilliped, must be relied on. The spine is definitely born by seven of the eight species of *Oratosquilla*, but was not mentioned for *O. massavensis*. Other species, *Squilla empusa*, *P. armata schizodontia*, *Alima hyalina*, and *Meiosquilla lebouri* have the spine, while *Harpiosquilla harpax* and *A. fasciata* definitely do not.

The development of epipods on five pairs of maxillipeds in older larvae appears to be a generic character of *Squilla* as most other genera bear four pairs of epipods.

Characters such as rostral length and spinulation, carapace and telson shape, size, and spinulation, and overall body size and appearance have been too variable within the limited number of species presently described to use them in defining generic associations of the larvae. Deriving characters which apply to the youngest larvae as well as the old will be difficult since far fewer characters are present in the early stage larvae, and the gross appearance of the young larvae is very similar due to the small degree of differentiation. Other characters such as antennular segmentation, mouthpart morphology, setation, spination of the maxillipeds, or the presence of ocular, antennular, epistomal, or basal uropodal spines may also need to be examined. The setation and spination of the first maxilliped may be of great value in defining alliances of the species as well as in making specific determinations. However, many more complete descriptions of the larval developments undergone by the various species must be accomplished before larval characters can be used in establishing generic relationships.

The postlarva of *Squilla empusa* exhibited the basic features of first stage postlarva as determined for other species by Alikunhi (1967). These include the absence of anterolateral spines on the carapace, the extremely poorly developed carination of the carapace, acutely pointed marginal denticles of the telson, and moveable apices of the submedian spines of the telson. As with the adult, the postlarva possesses the full complement of teeth on the raptorial dactylus, just as Alikunhi (1967) found. Furthermore, the five pairs of epipods found in the adult are also possessed by the postlarva. Other adult characters were developed upon the next molt. The dorsal carinations of the carapace were developed, the lateral processes of the exposed thoracic somites five through eight resembled those of the adult, the marginal denticles of the telson were not as acute, and the submedian spines were fixed. The abdominal spinal formula was still not equal to that of the adult. Nevertheless, after the postlarva had undergone its first molt more than enough characters were shared with the adult to make a definite determination of the species.

CONCLUSIONS

1. *Squilla empusa* undergoes nine pelagic stages before attaining the postlarval stage.
2. The last stage stomatopod larva and postlarva described by Faxon (1882) are not *S. empusa*.
3. Larvae of *S. empusa* may be identified by the spinules of the carapace and the intermediate denticles of the telson. Stages I and II possess four spinules on the lateral margin of the carapace and four intermediate denticles. The third to ninth stages are armed with six spinules on the lateral margin of the carapace. There are two anterior and three posterior spinules all ventrally directed, and one median spinule laterally directed. The telsons of stages III to IX have 8 to 10 intermediate denticles.
4. Rostral length and spinulation, carapace and telson size and spinulation, and overall body size and appearance probably are specific rather than generic characters.
5. The presence or absence of teeth on the dactylus of the second maxilliped, the presence or absence of a spine on the basis of the second maxilliped, and the number of epipods may all be useful characters in determining generic status of larvae belonging to the Squillidae. However, many more complete descriptions of the larval developments undergone by the various species are needed before larval characters can be used in establishing generic relationships.

ACKNOWLEDGMENTS

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VARIATION IN THE FOURBEARD ROCKLING, *ENCHELYOPUS CIMBRIUS*, A NORTH ATLANTIC GADID FISH, WITH COMMENTS ON THE GENERA OF ROCKLINGS

DANIEL M. COHEN[1] AND JOSEPH L. RUSSO[2]

ABSTRACT

Enchelyopus cimbrius, the fourbeard rockling, is a gadid fish living around the rim of the North Atlantic Ocean. It varies geographically in color pattern; anal, dorsal, and pectoral fin ray counts; and vertebral and gill racker counts. There is a lack of overall concordance in patterns of variation in color and meristics. Morphometric characters do not distinguish populations from different geographical areas, and the fourbeard rockling is considered to be a single species.

New distributional records include the Gulf of Mexico, West Greenland, and West Africa.

We classify the rocklings as a tribe, Gaidropsarini, of the subfamily Lotinae. Characters previously used to separate rocklings into five genera—skull shape, vomerine tooth patch shape, number and distribution of supratemporal pores, length of first dorsal fin ray, and size of jaw teeth—do not distinguish nominal genera. Number of snout barbels divides rocklings into three groups that we tentatively recognize as genera: *Gaidropsarus*, the threebeard rocklings, with two snout barbels; *Enchelyopus*, the fourbeard rockling, with three snout barbels; and *Ciliata*, the fivebeard rocklings, with four or more snout barbels. *Onogadus* and *Antonogadus* are referred to the synonymy of *Gaidropsarus*.

The correct generic name for the fourbeard rockling is *Enchelyopus* Bloch and Schneider 1801, with *Rhinonemus* Gill 1863 as a junior synonym. It is not preempted by *Enchelyopus* Gronovius 1760 in Zoarcidae, which was used in a work that was not consistently binominal.

The fourbeard rockling, *Enchelyopus cimbrius*, is a locally abundant gadid fish found around the margins of the North Atlantic Ocean. Although this fish has been recorded in the literature for more than 200 yr, many aspects of its biology are obscure. Adults are sedentary bottom dwellers taken at depths ranging from about 1 to 650 m [we have been unable to verify depth records to 1,325 m given by Goode and Bean (1896)]. There is some indication that seasonal offshore-onshore movements occur (Bigelow and Schroeder 1953; Tyler 1971). The pelagic larval stages are similar in appearance to young hakes (*Urophycis*) and sometimes occur in silvery swarms near the surface (Bigelow and Schroeder 1953).

Recent collections discussed in this paper show that fourbeard rocklings are more widely distributed than previously was known and that geographical variation is present. One of our objectives in this paper is to describe, compare, and evaluate geographical variation of selected characters and to show that a single species is represented throughout the range of the fish.

The rockling group of the family Gadidae, which is characterized by several distinctive features, recently was divided into five genera (Wheeler 1969), although most ichthyologists have recognized only three (albeit under a variety of names). The second of our objectives is to show that at present there are valid reasons for only three.

The fourbeard rockling is currently named *Enchelyopus cimbrius* by North American ichthyologists and *Rinonemus cimbrius* by Europeans. Our final objective is to show that *Enchelyopus* is the correct generic name.

METHODS

All observations were made on museum specimens listed in the Appendix. Counts of dorsal and anal fin rays and vertebrae were taken from X-ray photographs. Vertebral counts do not include the terminal ural element. Gill raker counts include all rakers on upper and lower arms of the first arch. Head pores were examined with the aid of a compressed air jet. Measurements and their

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statistical analysis are described under Body Proportions. Statistical tests were performed on the IBM 370-148[3] computer at The George Washington University, using computer programs written and maintained at the Systematics Laboratory, NMFS, NOAA, and following statistical methods presented by Zar (1974).

GEOGRAPHICAL VARIATION

The distribution of the fourbeard rockling may be summarized as the coastal waters of the North Atlantic. In the western Atlantic the species occurs in: West Greenland (new record); the northwestern Gulf of Saint Lawrence and around Newfoundland as well (Leim and Scott 1966 and this paper) to Cape Fear (about lat. 34°N) (Bigelow and Schroeder 1953); the northeast coast of Florida (Bullis and Thompson 1965); off the Florida Keys (new record); and in the northern Gulf of Mexico (new record). In the eastern Atlantic the species occurs: around Iceland (Saemundsson 1949) and the Faroes (Joensen and Taaning 1970); from northern Norway at about lat. 71°N in the Barents Sea and south along the coasts of Scandinavia (Andriyashev 1954); in the western Baltic (rarely to the Gulf of Finland, Svetovidov 1973); throughout the North Sea and around the British Isles to the northern Bay of Biscay (Wheeler 1969; Du Buit 1968); and off Cape Blanc, Mauritania (new record). It is not known from the Mediterranean. Figure 1 shows the approximate localities from which we have studied specimens. More detailed locality data are presented in the Appendix.

Sampling Areas

We have compared fish from the following geographical areas.

Gulf of Mexico. Only 3 localities are represented in our collections. These specimens are among the most darkly pigmented of any we have studied.

Southern Atlantic. Specimens taken from the South Carolina coast at about lat. 33°N to about lat. 29°N on the east coast of Florida, which is as far south as specimens have been caught in the western Atlantic outside of the Gulf of Mexico. There is no reason to doubt that this population is continuous with those farther north, and the northern boundary as here given is arbitrarily limited by available study material.

Intermediate. Fish caught in the vicinity of Cape Hatteras from about lat. 35°N to the vicinity of Norfolk Canyon at about lat. 37°N are included in

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

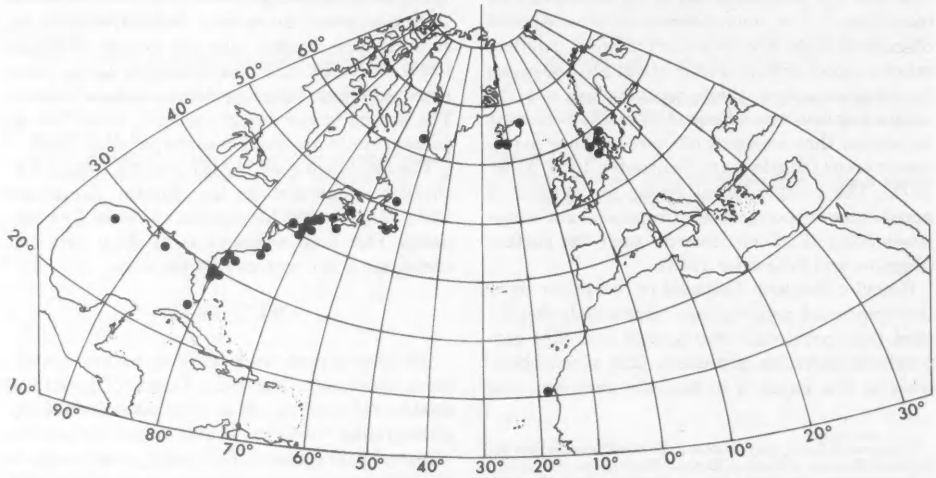

FIGURE 1.—Localities for our specimens of *Enchelyopus cimbrius*. Some dots represent more than one collection. For detailed data on localities see Appendix.

this area, which we separate because it is geographically between the region to the south, where fishes are mostly dark colored.

Northern Atlantic. This region extends along the western Atlantic coast from north of the vicinity of Norfolk Canyon to the northern North American limit of *E. cimbrius* occurrence.

Greenland. A single specimen from West Greenland is apparently the only known occurrence of *E. cimbrius* from Greenland.

Iceland. The region around Iceland.

Europe. Although *E. cimbrius* occupies a considerable area we have examined only a small sample, mainly from Denmark and Norway.

Africa. Two specimens from off the coast of Mauritania ca. lat. 21°N are the most southerly known.

Color

Enchelyopus cimbrius from the Gulf of Mexico and Southern Atlantic areas have on the average more of the dorsal fin colored with dark pigment than do fourbeard rocklings from other areas (Table 1). We have attempted to quantify this character by coding it on a 0-10 scale with 0 representing a fin with no dark pigment and 10 representing a fin that is completely dark. Values were subjectively assigned by a single observer (Cohen). Figure 2A shows a New England fish that would be coded as 1; Figure 2B shows the color pattern of a fish from the Gulf of Mexico, which would be coded as 6. Note that fish are morphologically intermediate and most variable in the Intermediate region[4] where the mean is 3.8 and the standard deviation is highest at 2.8.

Two other pigment characters were noted; however, neither was quantified. Fish with light fins lacked dark pigment in the groove along the base of the row of filaments between the strong first dorsal ray and the beginning of the normally developed dorsal fin (Figure 3A); fish with dark dorsal fins had varying amounts of dark pigment in this region (Figure 3B). Also, in many Gulf, Southern Atlantic, and Intermediate fish the body was dusky; in most others the body was a rather light straw color.

TABLE 1.—Frequency distributions of degree of dorsal fin pigmentation in *Enchelyopus cimbrius* from eight geographical areas. 0 = no dark pigment in dorsal fin; 10 = entire fin darkly pigmented.

	Degree of pigmentation													
Area	0	1	2	3	4	5	6	7	8	9	10	*N*	$\bar{x}$	*SD*
Gulf of Mexico				2	1	5	2	4	1	1	2	18	6.2	2.1
Southern Atlantic		1	—	2	6	1	6	17	6	6	2	47	6.7	1.9
Intermediate		7	6	4	6	—	—	2	1	3	1	30	3.8	2.8
Northern Atlantic		29	5	7	3	—	2					46	1.8	1.3
Greenland						1						1	5	—
Iceland		5	2	2	1							10	1.9	1.1
Europe	1	26	1	1	1	2						32	1.4	0.9
Africa		1	1									2	1.5	—

Meristics

Frequencies of both anal fin rays and dorsal fin rays show a pattern similar to, though less pronounced than, that shown by dorsal fin pigmentation in the western Atlantic (Tables 2, 3), with fish from the Intermediate area being intermediate between fish from the north and the south. Also, for anal fin rays the standard deviation is larger in fish from the Intermediate area than in adjacent samples. These two characters differ from dorsal pigmentation in having the highest mean in the Iceland sample.

Frequencies of pectoral fin rays and vertebrae for North American samples from the Intermediate area have nearly identical means in both

[4]Detailed descriptions of color variation in samples from Norfolk Canyon and comparisons with specimens from the northeast coast of Florida have been presented by: P. Szarek. 1974. A preliminary study of Norfolk Canyon *Enchelyopus cimbrius*. Ichthyology Term Paper, Virginia Institute of Marine Science.

TABLE 2.—Frequency distributions of numbers of anal fin rays in *Enchelyopus cimbrius* from eight geographical areas.

	Number of anal fin rays																
Area	36	37	38	39	40	41	42	43	44	45	46	47	48	49	*N*	$\bar{x}$	*SD*
Gulf of Mexico				6	4	2	4								16	40.2	1.2
Southern Atlantic				6	11	18	8	3							46	40.8	1.1
Intermediate				1	2	5	4	7	2	2	2	—	—	1	26	42.8	2.2
Northern Atlantic						8	8	9	13	9	2	2	1		52	43.5	1.7
Greenland								1							1	43	—
Iceland									2	4	3	1			10	45.3	0.9
Europe	1	—	1	1	—	2	1	3	6	1	—	—	—	1	17	42.6	3.0
Africa									1	1					2	44.5	—

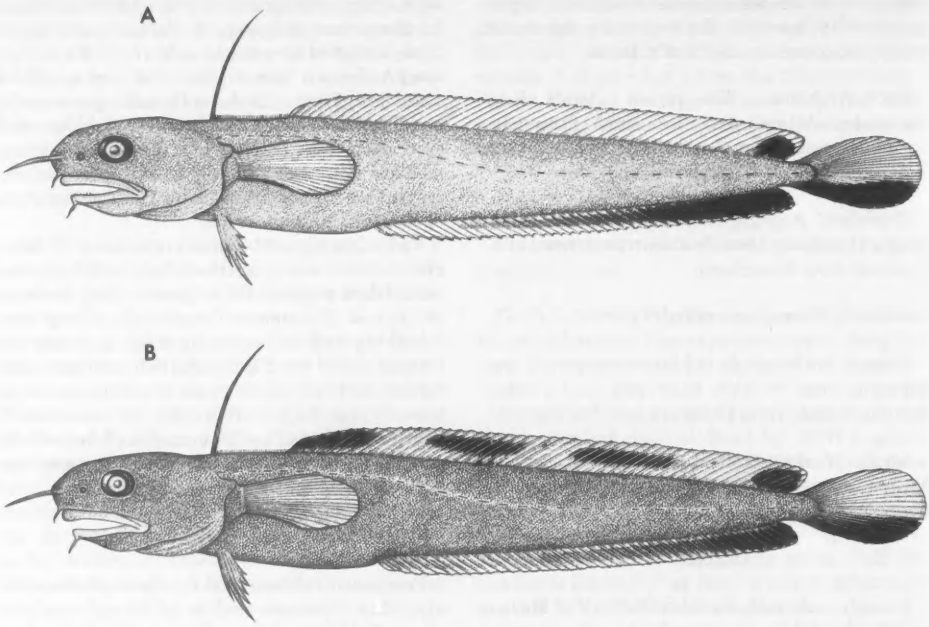

FIGURE 2.—*Enchelyopus cimbrius*. A, USNM 213501, standard length 282 mm, off Cape Cod, dorsal fin pattern coded as 1 (see text). B, color pattern of a fish from the Gulf of Mexico (USNM 217843) drawn on the outline of the fish shown in Figure 2A, dorsal fin pattern coded as 6 (see text).

TABLE 3.—Frequency distributions of numbers of dorsal fin rays in *Enchelyopus cimbrius* from eight geographical areas.

	Number of dorsal fin rays													
Area	45	46	47	48	49	50	51	52	53	54	55	*N*	$\bar{x}$	*SD*
Gulf of Mexico	1	1	11	3								16	47.0	0.7
Southern Atlantic	1	8	10	12	7	8	1					47	47.9	1.5
Intermediate			1	3	8	9	5	—	2	1		29	49.9	1.6
Northern Atlantic	1	—	—	6	13	8	12	4	4	3	1	52	50.4	1.9
Greenland							1					1	51	—
Iceland						5	2	3				10	50.8	0.9
Europe		1	2	3	3	4	3	1				17	49.2	1.7
Africa						2						2	50.0	—

of these characters with Northern Atlantic fish, rather than being intermediate (Tables 4, 5); however, for pectoral fin rays, fish from these two areas have lower counts that are in between Gulf and Alantic, and Greenland, Iceland, and Europe samples. Iceland fish average highest of all in dorsal and anal fin ray counts and in vertebral counts (not including the few specimens from Greenland and Africa). In pectoral counts, however, Iceland and Europe specimens have identical means.

In total gill raker counts (Table 6) eastern Atlantic samples have higher means than do western Atlantic samples, with the highest standard deviation being in the Northern Atlantic samples.

Body Proportions

Measurements were taken of the following eight body parts and compared for six of them in fish from the six geographical areas listed below and described previously under sampling areas (Greenland and Africa are not included in the present analysis). Linear regressions were calculated for the following dependent variables, with standard length as the independent variable:

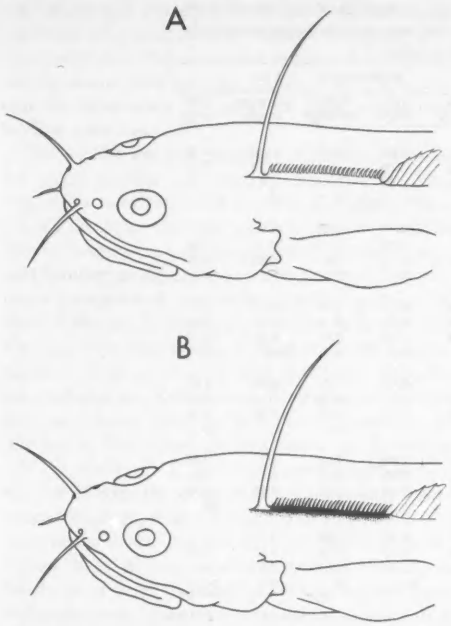

FIGURE 3.—*Enchelyopus cimbrius*. A, USNM 213501, head length 62.8 mm, off Cape Cod, note absence of dark pigment along base of fin with short rays. B, USNM 217843, head length 33.2 mm, Gulf of Mexico, note dark pigment along base of fin with short rays.

TABLE 4.—Frequency distributions of numbers of vertebrae in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of vertebrae									
	49	50	51	52	53	54	55	*N*	$\bar{x}$	*SD*
Gulf of Mexico			9	7				16	51.4	0.5
Southern Atlantic	1	1	18	22	10			52	51.8	0.9
Intermediate			4	7	12	6	1	30	52.8	1.0
Northern Atlantic			3	14	26	15	1	59	52.9	0.9
Greenland						1		1	54	—
Iceland					4	3	3	10	53.9	0.9
Europe			2	3	7	3		15	52.7	1.0
Africa						1	1	2	54.5	—

snout to first dorsal fin (pre D_1 distance); first dorsal fin to the dorsal fin beginning posterior to the row of small filamentous rays (D_1-D_3 distance); head length; pectoral fin length; upper jaw length; horizontal diameter of eye (orbit length); length of barbel on lower jaw; and ventral fin length. Numbers of specimens measured and their size ranges (standard length in millimeters) were: Gulf of Mexico 17 (125-228); Southern Atlantic 46 (125-263); Intermediate 29 (104-202); Northern Atlantic 53 (50.5-297); Iceland 10 (151-327); Europe 27 (93.8-300).

TABLE 5.—Frequency distributions of numbers of pectoral fin rays in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of pectoral fin rays							
	15	16	17	18	19	*N*	$\bar{x}$	*SD*
Gulf of Mexico	1	2	9	6	1	19	17.2	0.9
Southern Atlantic		9	21	14	1	45	17.2	0.8
Intermediate	2	9	14	4		29	16.7	0.8
Northern Atlantic	5	21	21	5	1	53	16.5	0.9
Greenland			1			1	17	—
Iceland	1	2	2	5		10	17.1	1.1
Europe	1	2	8	4	1	16	17.1	1.0
Africa		2				2	16	—

TABLE 6.—Frequency distributions of total numbers of gill rakers on first arch in *Enchelyopus cimbrius* from eight geographical areas.

Area	Number of gill rakers											
	5	6	7	8	9	10	11	12	13	*N*	$\bar{x}$	*SD*
Gulf of Mexico				5	3	2	—	1		11	9.0	1.3
Southern Atlantic			2	9	12	17	4			44	9.3	1.0
Intermediate			1	1	11	6	5			24	9.5	1.0
Northern Atlantic	3	1	1	8	8	12	6	2		41	9.1	1.8
Greenland					1					1	9	—
Iceland					2	5	2	1		10	10.2	0.9
Europe					6	4	3	1	1	15	10.1	1.3
Africa					1	—	1			2	10.0	—

Analysis of covariance was used to compare regression lines (Tables 7, 8) for six measurements that we have treated as linear based on a coefficient of determination (r^2) of 0.73 or higher (Table 8). Two measurements, ventral fin length and barbel length, had coefficients of determination ranging from 0.42 to 0.61 and were not further analyzed.

Fishes from all six geographical areas demonstrated overall coincidence at the 0.05 level of significance in two characters, head length and upper jaw length. Hypotheses concerning overall coincidence of regressions for the other characters were rejected and hypotheses concerning the equality of slopes and intercepts were simultaneously tested.

The hypothesis concerning the equality of slopes was rejected for the D_1-D_3 distance versus standard length regression lines. Regression data were

TABLE 7.—Significance of differences in six morphometric characters in *Enchelyopus cimbrius* from six geographical regions. Independent variable is standard length.

Dependent variable	*N*	Overall coincidence	Equality of slopes	Equality of intercepts
Pre D_1 distance	165	[1]0.0048	0.5342	[1,2]4.9×10^{-5}
D_1-D_3 distance	165	[1]0.0024	[1]0.0111	[1]0.0012
Head length	182	0.3004	—	—
Pectoral fin length	150	[1]0.0061	0.0617	[1]0.0011
Orbit length	166	[1,2]2.0×10^{-5}	0.1839	[1,2]2.4×10^{-6}
Jaw length	166	0.2892	—	—

[1]Rejection of hypothesis of equality at the 0.05 level of significance.
[2]Rejection of hypothesis of equality at the 0.001 level of significance.

TABLE 8.—*Y* intercepts in millimeters, slopes, coefficients of determination (r^2), and *N* for regression lines calculated on *Enchelyopus cimbrius* from six geographical areas. Independent variable is standard length.

Geographical area	Measurement					
	Pre D_1 distance	D_1-D_3 distance	Head length	Pectoral fin length	Upper jaw length	Orbit length
Gulf of Mexico:						
Y intercept	2.91	2.21	2.29	0.17	-3.08	0.10
Slope	0.16	0.12	0.18	0.14	0.11	0.04
r^2	0.89	0.86	0.93	0.87	0.87	0.79
N	16	16	17	14	17	17
Southern Atlantic:						
Y intercept	0.11	-4.74	0.22	-0.89	-1.83	0.76
Slope	0.17	0.15	0.20	0.15	0.11	0.04
r^2	0.96	0.89	0.94	0.91	0.89	0.90
N	43	44	46	43	44	44
Intermediate:						
Y intercept	-0.60	-0.74	-0.71	0.48	-2.69	-0.06
Slope	0.18	0.12	0.21	0.14	0.11	0.05
r^2	0.95	0.86	0.92	0.87	0.92	0.79
N	29	29	29	29	29	28
Northern Atlantic:						
Y intercept	-0.32	0.47	-0.43	-2.22	-3.38	1.64
Slope	0.18	0.12	0.21	0.16	0.12	0.04
r^2	0.97	0.89	0.97	0.92	0.87	0.92
N	51	51	53	38	51	50
Iceland:						
Y intercept	0.47	3.59	2.09	6.02	-5.71	2.65
Slope	0.17	0.10	0.20	0.12	0.13	0.03
r^2	0.79	0.92	0.99	0.87	0.98	0.98
N	10	10	10	10	9	10
Europe:						
Y intercept	-0.61	-4.37	-0.74	-2.06	-4.70	1.29
Slope	0.18	0.16	0.21	0.15	0.12	0.04
r^2	0.97	0.73	0.91	0.90	0.91	0.94
N	16	16	27	16	16	17

submitted to a Newman-Keuls multiple range test in order to determine which population sample or groups of population samples were different from others. This procedure failed to detect differences between any slopes, a not uncommon occurrence due to the fact that the analysis of covariance is a more powerful test than is the multiple range test. The sample from Iceland had the lowest slope at 0.10, the Northern Atlantic, Gulf of Mexico, and Intermediate samples each had a slope of 0.12, the Southern Atlantic sample had a slope of 0.15, and the sample from Europe had a slope of 0.16.

The hypotheses concerning the equality of *Y* intercepts was rejected at the 0.05 level of significance for all four characters tested. These regression data also were submitted to a Newman-Keuls multiple range test in order to determine which population sample or groups of population samples were different from others. Again, this procedure failed to detect significant differences between any *Y* intercepts.

If a more stringent 0.001 level of significance is used, only orbit length tests as being significantly different with respect to overall coincidence. Data for this regression from each of the six samples were submitted to a continuation of analysis of covariance to determine whether differences in the regression lines were attributable to the slopes and/or the *Y* intercepts. We accept equality of the slopes with a probability of 0.85. However we reject the equality of the *Y* intercepts after calculating a probability of equality of 2.06×10^{-5}. Regression data were submitted to a Newman-Keuls test, which failed to detect differences between any pairs of intercepts. Inspection of our data shows that rocklings from Iceland appear to have a proportionally larger eye than do other rocklings; however, our sample is small and may be biased by larger fishes; hence we do not draw inferences from this apparent difference.

Although differences between samples apparently exist, we do not interpret them as representing the kind of discontinuity that indicates distinct species. Their significance is beyond the scope of this paper.

Discussion

We believe that the fourbeard rockling is best considered as a single species throughout its entire range. Differences in pigment pattern, meristics, and the relative size of several body parts do exist; however, there are neither trenchant discontinuities in variation nor is there any overall

concordance in patterns of variation. Differences between and similarities among samples are summarized in Figure 4 and discussed below for meristics and color pattern. Differences in morphometric characters are so slight that we do not further consider them.

Gulf of Mexico and Southern Atlantic samples are quite similar, although at this time the two might be semi-isolated from each other. The clockwise loop current system in the Gulf of Mexico provides a possible pathway for the dispersal of young, pelagic stage rocklings out of the gulf; there is no present avenue for recruitment into the Gulf of Mexico. If the single rockling taken off the Florida Keys represents more than a stray, then perhaps Gulf of Mexico and Southern Atlantic populations are continuous; otherwise, the north Gulf-northeast Florida distribution pattern is similar to that noted first in fishes by Ginsburg (1952). Although *E. cimbrius* seems rare in the Gulf of Mexico its occurrence at two widely separated localities, with a collection of 16 individuals from one of them, indicates that the species is established there. Although pelagic stages have not yet been taken from the Gulf of Mexico or Southern Atlantic areas, it seems reasonable to assume that they occur there and are available for dispersal in the Gulf Stream system.

Rocklings from the Intermediate area are indeed intermediate between adjacent populations to the north and south in degree of pigmentation and in dorsal and anal ray counts. Furthermore, for two of these characters, color and number of anal fin rays, the standard deviation is larger than in other populations, implying that recruits from different spawning populations are entering the area or that the characters are genetic and variability is being maintained during spawning in the Intermediate area. For two characters, numbers of vertebrae and pectoral fin rays, Intermediate and Northern Atlantic fish are nearly identical and differ from Southern Atlantic and Iceland samples. These characters must be determined or mediated differently than are color pattern and dorsal and anal fin ray counts. Gill raker count appears to reflect still a third method of character determination as the means are different on the two sides of the Atlantic. Although pelagic early stages have not been taken in the Intermediate area, they may be available for dispersal to the northeast by means of the Gulf Stream and to the southwest in coastal currents that parallel the Gulf Stream. Such dispersal patterns would help to account for the occurrence of dark-colored rocklings in the north and light-colored ones in the south.

Rocklings from the Northern Atlantic area more closely resemble fish from Europe and Iceland in degree of pigmentation and number of vertebrae than they do their immediate neighbors to the south. Conversely they are closer to other North American samples in numbers of pectoral

CHARACTER	GEOGRAPHICAL AREA					
	Gulf	S. Atl.	Intermed.	N. Atl.	Iceland	Europe
Color	6.2	6.7	3.8	1.8	1.9	1.4
Anal Rays	40.2	40.8	42.8	43.5	45.3	42.6
Dorsal Rays	47.0	47.9	49.9	50.4	50.8	49.2
Vertebrae	51.4	51.8	52.8	52.9	53.9	52.7
Pectoral Rays	17.2	17.2	16.7	16.5	17.1	17.1
Gill Rakers	9.0	9.3	9.5	9.1	10.2	10.1

FIGURE 4.—Summary of means of character states for *Enchelyopus cimbrius* from six geographical areas. Heavy lines are drawn around entries that are discussed in the text as separate entries and that illustrate overall lack of convergence in character states.

rays and gill rakers. Spawning is known to occur in the Northern Atlantic area. Eggs have been taken from surface tows in Passamaquoddy Bay, where spawning peaked at bottom temperatures of 9° to 10°C (Battle 1930). In Long Island Sound eggs were found to be most abundant in the upper 12 m (Williams 1968). In reviewing the natural history of *E. cimbrius* in the Gulf of Maine, Bigelow and Schroeder (1953) mentioned the possibility of planktonic existence as long as 3 mo. Given such a time span, the complex hydrographic regime of the area might occasionally distribute early stages to the south inshore of the Gulf Stream or even more rarely might transport them via the Gulf Stream to the eastern Atlantic.

Iceland rocklings are usually light colored, as are fish from the Northern Atlantic and Europe areas. For counts of dorsal and anal fin rays, and vertebrae, Iceland fish have the highest means of all (ignoring the two fish from Africa); perhaps these characters are influenced by temperature, as Iceland has the lowest temperatures of any of the six areas. In numbers of pectoral rays, Iceland and European fish are identical and in gill rakers nearly so, and different from counts of North American ones. Adults at least of the Iceland population may be isolated as Kotthaus and Krefft (1967) did not catch *E. cimbrius* along the Iceland-Faroe ridge. *Enchelyopus cimbrius* spawns at least around the southwest coast of Iceland (Einarsson and Williams 1968).

The linear range of the fourbeard rockling along the coasts of Europe is about as great as along the coasts of North America. We have examined only a small sample, from southern Scandinavia; hence, it is possible that more variation exists than we have recorded. However, we point out that in our sample the color pattern resembles that of Iceland and Northern Atlantic fish, that counts of anal and dorsal fin rays and vertebrae are lower than those in Iceland, and that in numbers of pectoral fin rays and gill rakers Europe and Iceland fish are more like each other than they are like North American populations. Rocklings are known to spawn in European waters [Svetovidov (1973) gives several references]. *Enchelyopus cimbrius* could have reached Europe from the west via the Gulf Stream system; it seems unlikely that east to west dispersal is possible.

We do not know whether the West Greenland specimen of *E. cimbrius* represents a breeding population or a stray.

The two West African examples are so far removed from their nearest known neighbors (Bay of Biscay) that we forego conjecture as to their origin.

THE GENERA OF ROCKLINGS

The rocklings are classified in the subfamily Lotinae of the family Gadidae (Svetovidov 1948) and can be distinguished by the nature of the three dorsal fins, which, although scarcely separated from each other, bear quite different kinds of rays (Figure 5). The first dorsal fin consists of a single, unsegmented ray which is not bilaterally divided (we have examined microscopic sections) and is supported by a strong pterygiophore. The ray is thicker than any others in the dorsal fin and in many species is longer as well. In *Enchelyopus cimbrius* it is soft, being ossified only proximally. Sharply distinguished from the first and third dorsal fins is a row of small, unsegmented, bilaterally divided filaments which appear fleshy, although they stain with alizarin. These small rays originate on a compressed ridge that rises from a middorsal groove. Although Bogoljubsky (1908) followed by Svetovidov (1948) did not consider these filaments to be true fin rays they should be considered as such, as examination of an alizarin preparation and of sections shows that a simple, ossified, rod-shaped skeletal support is present for each. The third dorsal fin is composed of ordinary, bilaterally divided, segmented rays, each with a well-developed pterygiophore.

A second characteristic of the rocklings is the presence on the snout of prominent barbels (the closest approach to this character among other gadids being a nasal cirrus in *Lota*) in addition to the barbel at the tip of the lower jaw.

Thus, the rocklings are distinguished by two specialized characters and can be considered as a distinct tribe of Lotinae, the Gaidropsarini [classified as a distinct family by some, for example, de Buen (1934)].

Although rocklings have been treated under as many as 14 different generic names [see Svetovidov (1973) for synonyms], many ichthyologists (for example, Andriyashev 1954; Norman 1966) follow Svetovidov (1948) in recognizing three. More recently, however. five genera have been recognized (Wheeler 1969). How many genera should be recognized and why?

In his 1948 treatment of the rocklings, Svetovidov provided diagnoses for the three genera that he recognized based on barbel number, skull shape, vomerine tooth patch shape, and

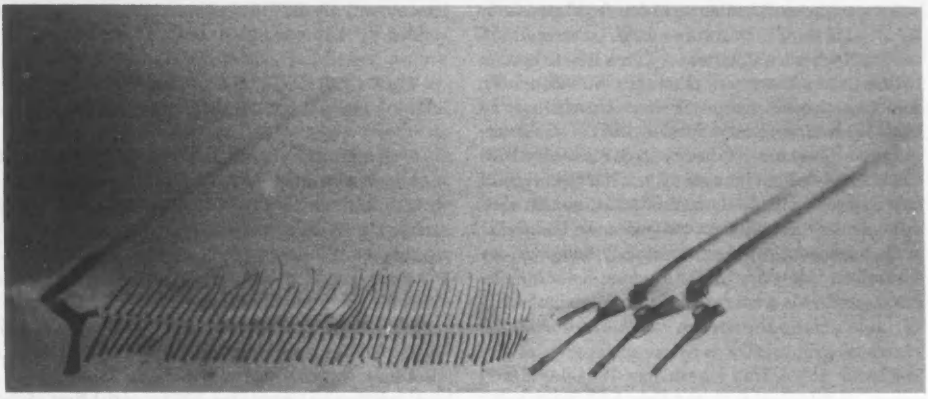

FIGURE 5.—*Enchelyopus cimbrius*, USNM 217900, standard length 135 mm; photograph of an alizarin preparation in glycerin showing the three different kinds of dorsal fin rays and their skeletal supports.

number and distribution of supratemporal pores (our Table 9). Unfortunately, he was unable to study all of the species. We have examined six of the nominal *Gaidropsarus* species that he recognized, both species of *Ciliata*, and, of course, *Enchelyopus* (study material of all genera is listed in the Appendix).

Number of barbels is the only character that unequivocally divides our material according to Svetovidov's classification.

Proper evaluation of the skull-width character will require the examination of osteological preparations, which we have not done. We note, however, that although *Ciliata mustela* has a notably broad skull, that of *C. septentrionalis* appears to be narrower. Also, although most species of *Gaidropsarus* appear to have narrow skulls, that of *G. guttatus* appears broad.

Regarding the size and shape of the vomerine tooth patch, it is highly variable, and although it may serve to distinguish some species it is of doubtful value at the genus level.

TABLE 9.—Summary of diagnostic characters for three rockling genera given by Svetovidov (1948).

Genus and no. of species	Characters			
	No. of barbels	Skull shape	Vomer	Supratemporal pores
Gaidropsarus (13)	3	Narrow	Head large, apex angular	3 = 1 pair + 1 median
Enchelyopus (1)	4	Narrow	Small	3 = 1 pair + 1 median
Ciliata (2)	5 or more	Broad	Head small, anterior a semicircle	2 = 1 pair

Number of supratemporal pores also is a variable character. Five of the *Gaidropsarus* species that we have studied show the pattern given for the genus by Svetovidov (1948), one median and one pair of pores (= 3). However, *G. argentatus* has two pairs and no median pores (= 4). In *Ciliata*, *C. mustela* has one pair (= 2), while *C. septentrionalis* has three pairs (= 6).

As noted above, Wheeler (1969) recognized five genera, the three recognized by Svetovidov (1948): *Enchelyopus*, *Ciliata*, and *Gaidropsarus*; and also *Onogadus* de Buen 1934; and a genus introduced for the first time, *Antonogadus*.

Onogadus was originally proposed for *Gaidropsarus ensis*, one of the threebeard rocklings, because of its elongate first dorsal ray. Wheeler (in Svetovidov 1973) has subsequently assigned to *Onogadus*, *G. argentatus*, a species with a far shorter first dorsal fin ray. We have found the length of the first dorsal fin to be highly variable in *Enchelyopus*. As presently used, this character does not separate genera. (Wheeler[5] has informed us that *Onogadus* may be differentiated on the basis of vertebral counts. Due to insufficient data we have no comment on this character.) As we have mentioned above, *G. argentatus* differs from *G. ensis* and resembles *Ciliata* in lacking a median supratemporal pore.

[5]A. Wheeler, Department of Zoology, British Museum (Natural History), Cromwell Road, London S.W. 7. England. Pers. Commun. March 1978.

Antonogadus Wheeler 1969 was first introduced in the combination *Antonogadus macrophthalmus* (Günther), unfortunately, in a key to species rather than a treatment of genera. Subsequently, another threebeard rockling, *Gaidropsarus megalokynodon* (Kolombatovic 1894), was referred to *Antonogadus* (Wheeler in Svetovidov 1973) in a checklist. There is no way to tell if the original key characters describing dentition, mouth size, and color are diagnostic of the genus *Antonogadus* or the species *A. macroptthalmus*; however, we assume that they apply to the genus. Color may be discounted as a generic character as it is highly variable among the species of *Gaidropsarus* and varies geographically in the single species of *Enchelyopus*. Regarding mouth size, Wheeler (1969) noted "mouth large, extending well past eye"; however, figures of *macrophthalmus* given by Günther [1867, pl. 5, fig. B and 1887, pl. 42, fig. D, the latter as *Onus carpenteri*, a junior synonym of *macrophthalmus* according to Wheeler in Svetovidov (1973)] show fish with small mouths. The second species referred to *Antonogadus, megalokynodon*, is figured by Söljan (1963) as having a large and capacious mouth, but he shows the same condition for several other species of threebeard rocklings. So far as we can tell mouth size is not a useful generic character. Carrying on to dentition, Wheeler (1969) noted, "A pair of large, fang-like, teeth (sometimes three or four) in front of the upper jaw." If *Antonogadus* is recognized on the basis of such a character then it would be necessary to place the two species of *Ciliata* in separate genera, as *C. mustela*, the type-species of the genus has bands of equal-sized teeth in the upper and lower jaws, while *C. septentrionalis* has in addition to these bands a much enlarged outer row of teeth in the upper jaw and an enlarged inner row in the lower jaw.

It is by no means clear that number of barbels alone divides the rocklings into natural species assemblages; convergence may have occurred and other groupings based on different characters may produce a phyletically more correct classification. Obviously, thorough study and a careful analysis of characters is required. For the present there seems insufficient information available to do other than recognize on the basis of number of barbels a single genus with three subgenera, or three genera. We follow the latter course as it is the most conservative in terms of the present usage of names. We recommend therefore, that for the present *Onogadus* be relegated once again to the synonymy of *Gaidropsarus* where it should be joined by *Antonogadus*.

THE CORRECT GENERIC NAME FOR THE FOURBEARD ROCKLING

Although differences at the species level have not evolved in populations of the fourbeard rockling on both sides of the North Atlantic, curiously enough geographical isolation seems to have affected the evolution of different generic names. *Rhinonemus* is used by European ichthyologists (see, for example, Svetovidov 1973); North American ichthyologists use *Enchelyopus* (see, for example, Leim and Scott 1966). Which is the correct name?

Enchelyopus Gronovius 1760 was the first of the two names proposed. Although only a brief color description was given, reference was made to the same author's pre-Linnean Museum Ichthyologicum published in 1754, in which work under the names *Mustela vivipera* and viviparous eelpout is presented a recognizable description of the species presently named *Zoarces viviparus* (Linnaeus). This identification is further verified by a Gronovius specimen still extant in the British Museum, which Wheeler (1958) has suggested is a type-specimen of *Blennius viviparus* Linnaeus. Use of *Enchelyopus* in Zoarcidae, where it is a senior synonym of *Zoarces* Cuvier 1829 has been accepted by Norman (1966) and noted as being correct by Andriyashev (1973). Some ichthyologists (Gill 1863b; Jordan 1917), however, seem to have overlooked Gronovius (1760) and attributed the name to Gronovius (1763) in his Zoophylaceum, a work subsequently ruled on by the International Commission on Zoological Nomenclature (Opinion 89) as being unavailable for purposes of zoological nomenclature. The Commission noted in its ruling that combinations used in the Zoophylaceum were "binary" though not "binomial," which interpretation complied with the then current edition of the Rules, and the work was declared unavailable by suspension of the Rules.

Although Gronovius (1760) never has been ruled on by the Commission it follows the same system of nomenclature as does Gronovius (1763) and clearly is not binominal. The same is true of Gronovius (1762), which has been rejected (Opinion 332). Under the provisions of the present Code (Article 11(c)), names published in Gronovius (1760) are not available as the author did not con-

sistently apply the principles of binominal nomenclature. Although Article 11.(c)(i) ("Uninominal genus-group names published before 1931 without associated nominal species are accepted as consistent with the principles of binominal nomenclature, in the absence of evidence to the contrary.") might serve as a basis for arguing that the names in Gronovius (1760) are available, the interests of stability would be served best by considering the work unavailable, as its acceptance would require not only that *Enchelyopus* Gronovius 1760 replace *Zoarces* Cuvier 1829, but also that *Cyclogaster* Gronovius 1760 replace *Liparis* Scopoli 1777.

If Gronovius (1760) is considered as unavailable for purposes of zoological nomenclature then the first valid use of *Enchelyopus* is by Bloch and Schneider (1801). The type-species was stated by Jordan (1917) as *Gadus cimbrius* Linnaeus 1766 as first restricted, and Svetovidov (1973) gave the type as *Gadus cimbrius* Linnaeus 1766 by monotypy. However, neither of these methods of type fixation is correct as Bloch and Schneider referred 12 species to the genus, and although *cimbrius* is the first one in order, there is no action that could be construed as a type designation. The earliest type designation for *Enchelyopus* Bloch and Schneider 1801 that we have been able to find is that of Jordan (1917) as *Gadus cimbrius* Linnaeus 1766.

Rhinonemus Gill (1863a) was proposed for *Motella caudacuta* Storer 1848, a junior synonym of *Gadus cimbrius* Linnaeus (Goode and Bean 1879) and is therefore a junior synonym of *Enchelyopus* Bloch and Schneider.

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APPENDIX

The following abbreviations indicate institutions or collections: CU, Cornell University; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National d'Histoire Naturelle, Paris; NEFC, Northeast Fisheries Center, Woods Hole, Mass.; NMC, National Museum of Natural Sciences, Ottawa; USNM, National Museum of Natural History, Washington, D.C.; ZMUC, Zoologisk Museum, Copenhagen. The "Intermediate" region, below, extends from about lat. 35°N to about lat. 37°N in the western Atlantic.

Enchelyopus cimbrius

GULF OF MEXICO—USNM 190346 (3 specimens), *Silver Bay* stn 294, 27°54′N, 95°23′W, 79 m. USNM 217843 (16), *Oregon* 3724, 29°04′N, 88°31′W, 403 m. USNM 217939 (1), *Oregon* 5795, 24°16′N, 82°30′W, 439 m.

SOUTHERN ATLANTIC—USNM 217923 (2), *Silver Bay* 1611, 29°06′N, 80°00′W, 339-384 m. USNM 217924 (2), *Silver Bay* 223, 29°14′N, 80°05′W, 247 m. USNM 217935 (1), *Oregon* 5798, 29°14′N, 80°05′W, 357 m. USNM 217933 (5), *Oregon* 5098, 29°17′N, 80°05′W, 379 m. USNM 217931 (1), *Silver Bay* 4227, 29°20′N, 80°05′W, 348 m. USNM 217949 (2), *Silver Bay* 224, 29°29′N, 80°09′W, 329 m. USNM 217937 (1), *Combat* 475, 29°30′N, 80°10′W, 293 m. USNM 217934 (3) *Oregon* 5093, 29°31′N, 80°09′W, 384 m. USNM 217932 (1), *Silver Bay* 219, 29°34′N, 80°09′W, 348 m. USNM 217917 (1), *Silver Bay* 1607, 29°34′N, 80°09′W, 371 m. USNM 217943 (1). *Combat* 325, 29°35′N, 80°10′W, 366 m. USNM 217936 (1), *Combat* 314, 29°38′N, 80°11′W, 329 m. USNM 217918 (1), *Oregon* 5238, 29°39′N, 80°12′W, 348 m. USNM 217916 (2), *Silver Bay* 1606, 29°40′N, 80°12′W, 348 m. USNM 217940 (1), *Silver Bay* 217, 29°41′N, 80°08′W, 348 m. USNM 217919 (2), *Silver Bay* 458, 29°49′N, 80°10′W, 220 m. USNM 217921 (2), *Silver Bay* 1552, 29°43′N, 80°12′W, 302 m. USNM 217948 (1), *Combat* 435, 29°46′N, 80°12′W, 366 m. USNM 217920 (1), *Silver Bay* 3742, 29°50′N, 80°13′W, 275 m. USNM 217950 (5), *Silver Bay* 1604, 29°50′N, 80°10′W, 302 m. USNM 217947 (2), *Silver Bay* 3678, 29°53′N, 80°11′W, 329 m. USNM 217944 (3), *Silver Bay* 3675, 29°55′N, 80°11′W, 329 m. USNM 217922 (1) *Silver Bay* 4367, 29°55′N, 80°11′W, 320m. USNM 217945 (1), *Oregon* (1), 5233, 29°54′N, 80°10′W, 348 m. USNM 217925 (1), *Combat* 471, 29°57′N. 80°12′W, 329 m. USNM 217946 (3), *Pelican* 182-8, 32°09′N, 79°02′W, 275 m. USNM 217938 (1), *Combat* 300, 32°15′N, 78°51′W, 348 m. USNM 217927 (1), *Combat* 289, 33°03′N, 77°09′W, 366 m.

INTERMEDIATE—USNM 45898 (1), *Albatross*, 35°40′N, 74°52′W. USNM 45895-6 (7), *Albatross*, 36°02′N, 74°48′W. USNM 217941 (1), *Oregon II* 10763, 36°01′N, 74°48′W, 311-567 m. USNM 217951 (1), *Oregon II* 10664, 36°12′N, 74°47′W, 249-329 m. USNM 217942 (2), *Oregon II* 10724, 36°14′N, 74°45′W, 366-421 m. USNM 217929 (2), *Columbus Iselin* 73-10-40, 36°33′N, 74°42′W, 296 m. USNM 217928 (3), *Columbus Iselin* 73-10-47, 36°37′N, 74°42′W, 316 m. USNM 217926 (3), *Columbus Iselin* 73-10-89, 37°02′N, 74°38′W, 367 m. USNM 217930 (7), *Columbus Iselin* 73-10-73, 37°05′N, 74°43′W, 194-479 m.

NORTHERN ATLANTIC—USNM 28994 (1), *Albatross*, 38°39′N, 73°11′W, 238 m. USNM 45969 (1), *Albatross*, 38°54′N, 72°51′W. USNM 28917 (1), 39°43′N, 71°32′W. USNM 45891 (1), *Albatross*, 39°48′N, 71°49′W. MCZ 37492 (1), *Capt. Bill II* 20, 39°57′N, 71°07′W, 412 m. USNM 28843 (1), *Fish Hawk*, 39°57′N, 70°32′W. USNM 28816 (1), 39°N, 71°W. MCZ 38039 (1), *Caryn* 3-1, 39°59′N, 70°48′W, 381 m. USNM 33352 (1), *Fish Hawk*, 40°20′N, 70°35′W. USNM 28709 (1), 40°24′N, 70°42′W. USNM 35680 (1), 40°21′N, 70°29′W. USNM 28890 (2), 40°28′N, 70°44′W. USNM 126948 (1), *Fish Hawk*, Long Island Sound, 22 m. USNM uncat. (1), *Albatross IV*, 41°14′N, 71°41′W. USNM 213501 (7), *Blesk* 68-18, 22-01, 41°52′N, 68°12′W, 198 m. USNM uncat. (1), *Blesk* 68-18, 24-02, 41°36′N, 68°52′W, 138 m. USNM uncat. (1), *Blesk* 68-18, 28-01, 42°N, 69°39′W, 210 m. USNM 16656 (1), Woods Hole, Mass. CU 18353 (3), *Albatross III* 27-45, 41°53′N, 69°10′W, 212 m. USNM uncat. (1), *Delaware* 60-1-11, 41°52′N, 68°14′W, 227 m. CU 18274 (1), *Albatross III* 61-1, 41°49′N, 68°14′W, 154 m. USNM 23761 (1), Provincetown, Mass. CU 45869 (1), *Albatross IV* 63-5-69, 42°07′N, 67°31′W. NEFC uncat. (3), *Albatross III* 70-23, 42°10′N, 68°38′W, 183 m. NEFC uncat. (1), *Albatross III* 101-103, 42°15′N, 67°10′W, 168 m. CU 23620 (3), *Albatross III* 27-55, 42°41′N, 69°49′W, 256 m. NEFC uncat. (1), *Albatross III* 47B-3-2, 42°41′N, 70°09′W, 84-139 m. USNM 83925 (1), Mass. Bay. USNM 21918 (1), Mass. Bay,

134 m. USNM 131920 (6), Mass. Bay. USNM 21918-9 (2), Mass. Bay. MCZ 34614 (3), 42°56′N, 70°18′W, 165 m. MCZ 34611 (3), *Albatross II*, 43°07′N, 70°10′W, 154 m. USNM 37847 (1), Ipswich Bay, Mass. MCZ 34612 (9), *Albatross II*, 43°03′N, 70°09′W. USNM 45897 (1), *Albatross*, 43°34′N, 63°56′W. MCZ 34613 (4), 43°39′N, 68°12′W, 192 m. MCZ 12340 (1), Eastport, Maine. USNM 39060 (1), Prince Edward Island. USNM 43229 (1), 47°15′N, 53°58′W. NMC 63-151 (1), 51°28′N, 53°52′W.

GREENLAND—ZMUC uncat. (1), *Adolf Jensen* 4420, 64°22′N, 52°54′W, 460-540 m.

ICELAND—ZMUC 95-96, (2), North coast of Iceland, ca. 66°N, 18°30′W. ZMUC 830-32 (3), Vestman Islands. ZMUC 26-27 (2), 63°46′N, 22°56′W. ZMUC P379 (1), south of Iceland. USNM 217909 (1), 65°37′N, 21°00′W, 110 m. USNM 217911 (1), 65°41′N, 21°20′W, 137-152 m.

EUROPE—USNM 39724 (1), Denmark. ZMUC 84-85 (2), 90-93 (4), 501, 503-4 (3), P37284-292 (9), P37294-96 (3), P37298 (1), Denmark. ZMUC P37283 (1), Limfjord, Denmark. P37297 (1). Kallundborg Fjord, Denmark. ZMUC 88 (1), 502 (1), Snekkersten, Denmark. ZMUC 86 (1), 98 (1), Oresund, Denmark. ZMUC 22-23 (2), Skagerak, 200 m. ZMUC 25 (1), off Lindesnøs, Norway, 220 m. USNM 44514 (1), Drobak, Norway.

AFRICA—MNHN 38-110/111 (2), off Cape Blanc, Mauritania.

Ciliata mustela

USNM 130840 (4), Europe. USNM 44510 (1), Norway. USNM 216711 (2), Oresund, Denmark.

Ciliata septentrionalis

ZMUC 371656-7 (2), Faroe Islands.

Gaidropsarus argentatus

MCZ 38353,38387 (2), western North Atlantic. USNM 217907 (1), Iceland. USNM 217912 (1), Iceland. USNM 217910 (1), Spitsbergen. USNM 217908 (2), Iceland.

Gaidropsarus ensis

MCZ 37554 (1), western North Atlantic. MCZ 27882 (1), western North Atlantic. MCZ 38425 (1), western North Atlantic. MCZ uncat. (1), western North Atlantic. USNM 217913 (1), western North Atlantic.

Gaidropsarus guttatus

USNM uncat. (2), (1), (5), San Miguel Island, Azores.

Gaidropsarus mediterraneus

USNM uncat. (1), Tunisia.

Gaidropsarus vulgaris

USNM uncat. (1), (1), (3), Tunsia.

Gaidropsarus sp.

USNM uncat. (5), Amsterdam Island.

EARLY DEVELOPMENT OF SEVEN FLATFISHES OF THE EASTERN NORTH PACIFIC WITH HEAVILY PIGMENTED LARVAE (PISCES, PLEURONECTIFORMES)

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ABSTRACT

Eggs and larval series are described for six species of flatfishes occurring off California with heavily pigmented larvae. These are the pleuronectids *Pleuronichthys coenosus, P. decurrens, P. ritteri, P. verticalis,* and *Hypsopsetta guttulata* and the bothid, *Hippoglossina stomata*. A brief description of postflexion larvae of the Gulf of California species, *P. ocellatus*, is also presented.

Eggs of *Pleuronichthys* are unusual among flatfishes in possessing a sculptured chorion composed of a network of polygonal walls, whereas the chorions of *Hypsopsetta guttulata* and *Hippoglossina stomata* eggs are smooth and unornamented. Eggs of *Hypsopsetta guttulata* and *P. ritteri* are unusual among those of pleuronectid flatfishes in possessing an oil globule.

A combination of pigmentation, morphology, and meristics can distinguish the seven species of flatfishes with heavily pigmented larvae. Larvae of two species, *H. guttulata* and *P. decurrens*, have a distinctive pterotic spine on either side of the head. Sizes at hatching, at fin formation, and at transformation are important considerations to distinguish these species. Meristic counts, particularly of precaudal and caudal groups of vertebrae, are important to relate a larval series to its juvenile and adult stages and thus substantiate identification of the series.

This report deals primarily with the eggs, larvae, and early juveniles of flatfishes of the genus *Pleuronichthys*. Descriptions are included for complete series of larvae of four species, *P. decurrens* (curlfin turbot),[2] *P. coenosus* (C-O turbot), *P. verticalis* (hornyhead turbot), and *P. ritteri* (spotted turbot). A brief account of postflexion larvae of the Gulf of California species, *P. ocellatus* (Gulf turbot), is also given. Larvae of *Pleuronichthys* are heavily pigmented, even at hatching, as are those of the pleuronectid, *Hypsopsetta guttulata* (diamond turbot), and the bothid, *Hippoglossina stomata* (bigmouth sole). To identify heavily pigmented flatfish larvae obtained in plankton collections from the eastern North Pacific, it is necessary to know the larval developmental series of all of the above species. These species comprise minor incidental catches within California commercial and sport fisheries and are reported as a general grouping of "turbots." Species most commonly caught in the fisheries are *P. decurrens, P. coenosus, P. verticalis*, and *Hypsopsetta guttulata* (Frey 1971; Bell 1971; Oliphant 1973; Pinkas 1974; McAllister 1975). No specific catch data are available for *Hippoglossina stomata*, but the species is probably caught incidentally and included in the "miscellaneous sole" category of catch data.

In a review of the genus *Pleuronichthys*, Fitch (1963) recognized six species including the five listed above and *P. cornutus* from off Japan and China. In an earlier review of the genus, Starks and Thompson (1910) recognized these six species and *P. nephelus* Starks and Thompson. Norman (1934) concurred with Starks and Thompson in recognizing seven species. Fitch (1963), however, agreed with Hubbs (1928) in finding no grounds for the separation of *P. nephelus* from *P. coenosus* after his examination of the type material of *P. nephelus*. Fitch's review is thorough; he examined more than 5,700 individuals of the genus. We follow his classification.

The first descriptions of the eggs and early-stage larvae of *Pleuronichthys* were given by Budd (1940) who dealt with *P. coenosus, P. decurrens*, and *P. verticalis*. Orton and Limbaugh (1953) described the eggs of *Hypsopsetta guttulata* and *P.*

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[2]The common name turbot is used for all species of *Pleuronichthys*, a usage consistent with Fitch (1963), Miller and Lea (1972), and Gates and Frey (1974:79). The American Fisheries Society's list of common names (Bailey et al. 1970) designates *P. coenosus* and *P. decurrens* as soles, but we disagree with giving species within a genus different common general names.

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ritteri. Larvae of *P. verticalis* were illustrated in Ahlstrom and Moser (1975), and Eldridge (1975) described and illustrated larvae of *H. guttulata*.

MATERIALS AND METHODS

Eggs, larvae, and some juveniles were primarily obtained from California Cooperative Oceanic Fisheries Investigations (CalCOFI) collections. These samples were preserved in a consistent manner as described in Kramer et al. (1972). Additional material was obtained from bay, estuarine, and coastal collections of Occidental College; Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service; California State University at Fullerton; Scripps Institution of Oceanography; Oregon State University; and Humboldt State University. Specimens of *P. ritteri*, *P. verticalis*, and *H. guttulata* reared at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, were also utilized.

Egg and oil globule diameters were measured using an ocular micrometer in a stereomicroscope. For eggs that were not perfectly round, the greatest diameter was recorded. Scanning electronmicrographs were made for four kinds of *Pleuronichthys* eggs and for eggs of *Synodus lucioceps* (Synodontidae). The greatest diameter of 10 randomly selected polygonal facets of the chorion of *Pleuronichthys* and *Synodus* eggs were measured using an ocular micrometer in a compound microscope. To do this the chorion was cut into pieces that were laid flat on a glass slide with a cover slip over them.

The number of specimens examined varied by species, depending on their availability and abundance, ranging from several hundred larvae of *P. verticalis*, the most abundant species, to two larvae of *P. ocellatus*. For most species, the minimum number of specimens studied is indicated in the morphometric tables with usually twice as much material looked at for pigmentation development. A developmental series of larvae through juveniles was assembled for each species. Measurements of selected body parts were taken to provide descriptive and comparative morphometric data. Measurements were made on the right side of each pleuronectid specimen, and on the left side of the bothid, *Hippoglossina stomata*, using an ocular micrometer in a stereomicroscope. Terminology used in the morphometric tables is as follows:

Body length = In preflexion and flexion stages, horizontal distance from tip of snout to tip of notochord, referred to as notochord length (NL); in postflexion stages, from tip of snout to posterior margin of hypural elements, i.e., standard length (SL).

Snout to anus = Horizontal distance from tip of snout through midline of body to vertical through anus.

Head length = Horizontal distance from tip of snout through midline of head to margin of cleithrum preceding the pectoral fin base.

Snout length = Horizontal distance from tip of snout to anterior margin of pigmented region of eye.

Eye width = Horizontal distance through midline of pigmented eye.

Eye height = Vertical distance through center of pigmented eye.

Body depth at pectoral base = Vertical distance across body at pectoral fin base prior to formation of dorsal fin pterygiophores. An asterisk follows this measurement in the morphometric tables when it includes the depth of dorsal fin pterygiophores.

Body depth at anus = Vertical distance across body at anus prior to formation of dorsal fin pterygiophores. An asterisk follows this measurement when it includes the depth of the dorsal fin pterygiophores.

Caudal peduncle depth = Vertical distance across tail immediately posterior to terminal dorsal and anal fin rays.

Caudal peduncle length = Medial horizontal distance from vertical through terminal dorsal and anal fin rays to posterior margin of hypural elements.

Snout to pelvic fin origin = Horizontal distance from tip of snout to vertical through origin of right pelvic fin (left in *H. stomata*).

Larval specimens for each species were not available in sufficient numbers to clear and stain for complete data on meristics and sequence of ossification of bony elements. However, fin ray counts were made and tabulated on unstained specimens. A partial larval series of *P. verticalis*, our most abundant species, was cleared with KOH and stained with Alizarin Red-S by Hollister's method (1934) to determine the process of axial skeletal development and fin formation. In addition, several larvae of *P. coenosus* and *P. decurrens* were cleared and stained for precaudal and

total vertebral counts which verified identifications and proved that Budd (1940) confused identifications of larvae of these two species. Radiographs of transforming larvae, juveniles, and adults of each species provided additional meristic data.

We divide the larval period into three stages, preflexion, flexion, and postflexion, based on the flexion of the notochord which occurs during caudal fin formation (Moser and Ahlstrom 1970; Ahlstrom et al. 1976; Moser et al. 1977). In *Pleuronichthys* and some other flatfishes the initiation of caudal fin formation begins while the notochord is still straight, in the late preflexion stage; we designate this phase as "early caudal formation." We found it convenient to divide the flexion stage into three substages, early flexion, midflexion, and late flexion, dependent upon the state of flexion of the notochord. In the early flexion stage, the notochord is very slightly flexed upward; in midflexion, it is flexed midway (nearly a 45° angle); and in late flexion, the notochord is approaching a terminal position, except that the caudal rays remain in a slightly oblique position. Transformation from the larval to juvenile stage was marked by eye migration, development of ossified pectoral fin rays, scales, and the lateral line.

MERISTIC COUNTS OF LARVAE

Meristic counts overlap among species considered here, and for discrimination of species it is necessary to use a combination of counts (Table 1). Precaudal and caudal vertebral counts, used in conjunction with dorsal and anal fin counts, are of most use in relating larvae to juveniles or adults. Pelvic fin ray counts are six per side in all seven species and branchiostegal ray counts are seven per side. Pectoral fin counts cannot be made on larvae since ossified pectoral rays form at metamorphosis. Gill rakers are not fully formed during the larval period in the species described.

DESCRIPTION OF EGGS

Pleuronichthys spp.

Eggs of three *Pleuronichthys* species were first described by Budd (1940) who collected them in plankton hauls from Monterey Bay, Calif. Budd noted the hexagonal patterns on the chorions of *Pleuronichthys* eggs. This type of ornamentation of the egg shell is confined to *Pleuronichthys* among flatfishes, but similar polygonal sculpturing is found on eggs of the families Synodontidae (Sanzo 1915; Mito 1961) and Callionymidae (Holt 1893; Ehrenbaum 1905; Mito 1962) and in a more exaggerated form on eggs of the sternoptychid, *Maurolicus muelleri* (Sanzo 1931; Mito 1961), and the macrourid, *Coelorhynchus coelorhynchus* (Sanzo 1933). Eggs of the three species of *Pleuronichthys* described by Budd were strikingly different in size; his largest, *P. coenosus*, averaged 1.88 mm in diameter, his intermediate-sized egg, *P. decurrens*, 1.44 mm, and his smallest, *P. verticalis*, 1.07 mm. All had homogeneous yolk, and lacked an oil globule. Our work shows that Budd misidentified the two larger eggs and corresponding larvae; the one he called *P. coenosus* is *P. decurrens* and vice versa. Orton and Limbaugh (1953) described an egg with an hexagonal pattern on its chorion that possessed a single oil globule; they tentatively, but correctly, assigned it to *P. ritteri*. White (1977) illustrated a developing egg of *P. ritteri* from Newport Bay, Calif.

Information concerning egg diameters, presence or absence of an oil globule, and character of the chorion are given in Table 2 for six of the seven species treated in this paper. Egg diameters do not change noticeably with the duration of preservation, although some shrinkage is known at the initial time of preservation. There is no overlap in egg size for the three species of *Pleuronichthys* that lack an oil globule. Eggs of *P. decurrens* range from 1.84 to 2.08 mm; those of *P. coenosus*, from

TABLE 1.—Meristics of the seven species of flatfishes in the eastern North Pacific that have heavily pigmented larvae.[1]

Species	Dorsal rays	Anal rays	Pectoral rays (eyed side)	Vertebrae			Total gill rakers	Caudal rays	
				Precaudal	Caudal	Total		Total	Branched
Pleuronichthys decurrens	67-81	46-55	10-14	*14*-15	24-26	38-41	9-12	*19*-21	12-15(*13*)
P. coenosus	66-78	44-56	9-12	12-*13*	24-26	37-39	11-15	18-20(*19*)	12-15(*13*)
P. verticalis	66-79	44-51	10-12	13	23-25	36-38	9-11	*19*-20	12-14(*13*)
P. ocellatus	62-74	44-53	10-12	12-13	22-24	34-36	10-14	19	12-15(*13*)
P. ritteri	62-72	43-52	9-11	12-13	22-24	34-36	12-17	18-*19*	*13*-14
Hypsopsetta guttulata	65-75	47-55	11-13	11-*12*	22-24	34-36	?+[2](5-6)	*19*-20	13
Hippoglossina stomata	63-70	47-55	11-12	*11*	26-28	37-39	15-21	17½-*18½*	11-*13*

[1]Meristics compiled in Table 1 are derived in part from literature, particularly Fitch (1963), Norman (1934), Townsend (1936), Clothier (1950), and Ginsburg (1952), and in part from our original counts. Where a range is given and one count is predominant, that count is italicized.
[2]Lower limb count only.

TABLE 2.—Measurements of eggs of *Pleuronichthys* species, *Hypsopsetta guttulata*, and *Hippoglossina stomata*, including *Synodus lucioceps* for comparative data.

Species	Character of chorion	No. of eggs measured	No. of samples	Egg diameters (mm)			Oil globule diameters (mm)		
				Range	Mean	SD	Range	Mean	SD
Pleuronichthys decurrens	Sculptured	41	28	1.84-2.08	1.97	0.058	—	—	—
P. coenosus (CalCOFI)	Sculptured	20	15	1.28-1.56	1.47	0.066	—	—	—
P. coenosus (King Harbor)	Sculptured	287	2	1.20-1.42	1.29	0.047	—	—	—
P. verticalis	Sculptured	188	19	1.00-1.16	1.09	0.040	—	—	—
P. ritteri	Sculptured	82	13	0.94-1.08	1.01	0.029	0.08-0.14	0.10	0.009
Hypsopsetta guttulata	Smooth	35	4	0.78-0.89	0.84	0.027	0.12-0.14	0.13	0.010
Hippoglossina stomata	Smooth	26	9	1.22-1.38	1.29	0.045	0.20-0.26	0.23	0.018
Synodus lucioceps	Sculptured	168	8	1.20-1.48	1.32	0.049	—	—	—

1.20 to 1.56 mm; and those of *P. verticalis*, from 1.00 to 1.16 mm. Although eggs of *P. ritteri*, ranging in diameter from 0.94 to 1.08 mm, fall within the size range of *P. verticalis*, they can be readily distinguished by the presence of a small oil globule, 0.08-0.14 mm in diameter. Eggs of *P. ocellatus* were unavailable.

Differences in mean diameter of *P. coenosus* eggs were noted by locality, with eggs taken in open waters off the coast having a larger mean diameter and standard deviation (Table 2, CalCOFI collections) than eggs sampled from the inlet of a small, shallow, manmade harbor near a power plant discharge (Table 2, King Harbor samples). Except that they are often slightly larger in size, early- and middle-stage eggs of *P. coenosus* are difficult to differentiate from *Synodus lucioceps* eggs. They can be separated, however, by careful examination of the size and arrangement of polygons on the chorion. The mean of the greatest distance across polygons (sample size = 200 polygons) on *P. coenosus* eggs is 0.035 mm in contrast to 0.047 mm for *S. lucioceps* eggs (Table 3). Furthermore, the polygons on *P. coenosus* eggs are more regular in arrangement than on *S. lucioceps* eggs (Figure 1). This more uniform compacting of smaller polygons on *P. coenosus* eggs versus a more random patterning of larger polygons on *S. lucioceps* eggs is visible under a light microscope, and will separate these eggs. Late-stage eggs are easily distinguished by the heavy pigmentation on the embryo of *P. coenosus* compared with the sparse pigment on advanced *S. lucioceps* embryos, which also have a longer gut.

TABLE 3.—Comparison of polygon size on chorion of eggs of *Pleuronichthys* and *Synodus lucioceps*.

Species	No. of eggs measured	No. of polygons measured	Range of diameters (mm)	Mean (mm)	SD (mm)
Synodus lucioceps	20	200	0.038-0.053	0.047	0.0033
Pleuronichthys coenosus	20	200	0.029-0.043	0.035	0.0029
P. decurrens	2	20	0.038-0.046	0.042	0.0021
P. verticalis	2	20	0.037-0.051	0.042	0.0046
P. ritteri	2	20	0.028-0.032	0.030	0.0011

The arrangement of polygons on the chorion of eggs of the other three species of *Pleuronichthys* from the eastern Pacific is similarly uniform (Figure 2). The polygons are somewhat larger on the chorion of eggs of *P. decurrens* and *P. verticalis* than *P. coenosus*, averaging ca. 0.042 mm in both species (Table 3). Interestingly, Budd (1940) gave the identical value, 0.042 mm, for this measurement on eggs of these two species. The polygons are smaller on eggs of *P. ritteri*, averaging 0.030 mm.

The eggs of *P. cornutus* were described by Mito (1963) and Takita and Fujita (1964). Mito gave the egg diameters as 1.16-1.26 mm, the oil globule as 0.016-0.020 mm. Takita and Fujita gave similar measurements for the hexagonal meshes of 0.018 mm, but gave a smaller egg diameter of 1.03-1.11 mm.

Hypsopsetta guttulata

Orton and Limbaugh (1953) obtained running ripe eggs of *H. guttulata* by stripping ripe adults and obtained similar eggs from plankton collections. The eggs were notable in that they contained a conspicuous, moderately large oil globule. This was the first record of an oil globule in eggs of flatfishes of the family Pleuronectidae, subfamily Pleuronectinae. The egg capsule was simple, without polygonal sculpturing or other apparent texture; the yolk was homogenous. Orton (1953) gave a fairly detailed description of pigment development on embryos of *H. guttulata*. Neither of the above papers contained information on egg size. Eldridge (1975) reported a mean egg diameter of 0.80 mm with usually one oil globule of 0.14 mm in mean diameter and numerous other small oil globules in the yolk. Eggs in our samples had a mean diameter of 0.84 mm (range 0.78-0.89 mm) with a single oil globule averaging 0.13 mm in

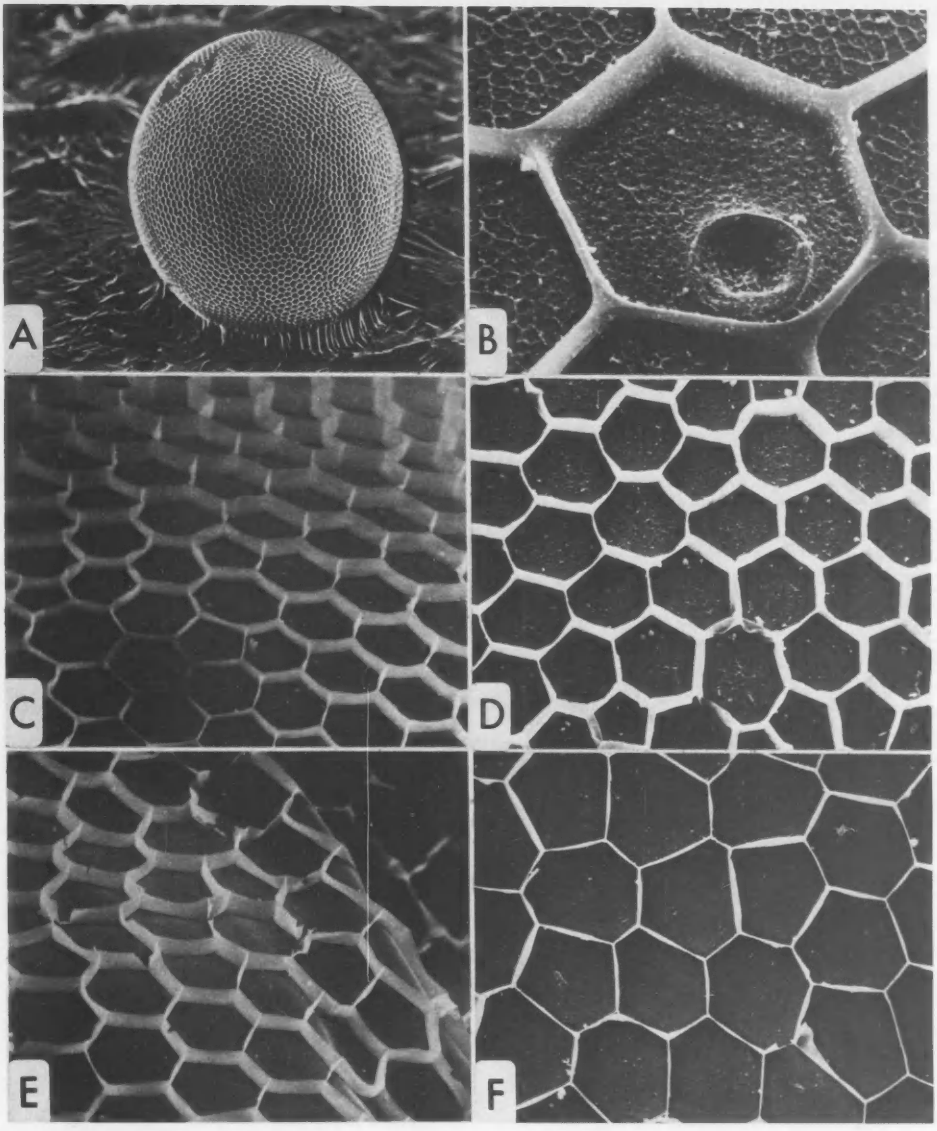


FIGURE 1.—Scanning electronmicrographs of *Pleuronichthys* and *Synodus lucioceps* eggs. A. Entire egg of *P. coenosus*, 40×; B. Single polygon from same egg showing micropyle and texture of chorion surface, 1,880×; C. Side view of same egg showing polygons in perspective and micropyle at lower left, 420×; D. Face view of same egg, 480×; E. Side view of *S. lucioceps* egg showing polygons in perspective, 455×; note delicate nature of polygons; F. Face view of same egg showing irregular nature of polygons and smooth surface of chorion, 490×.

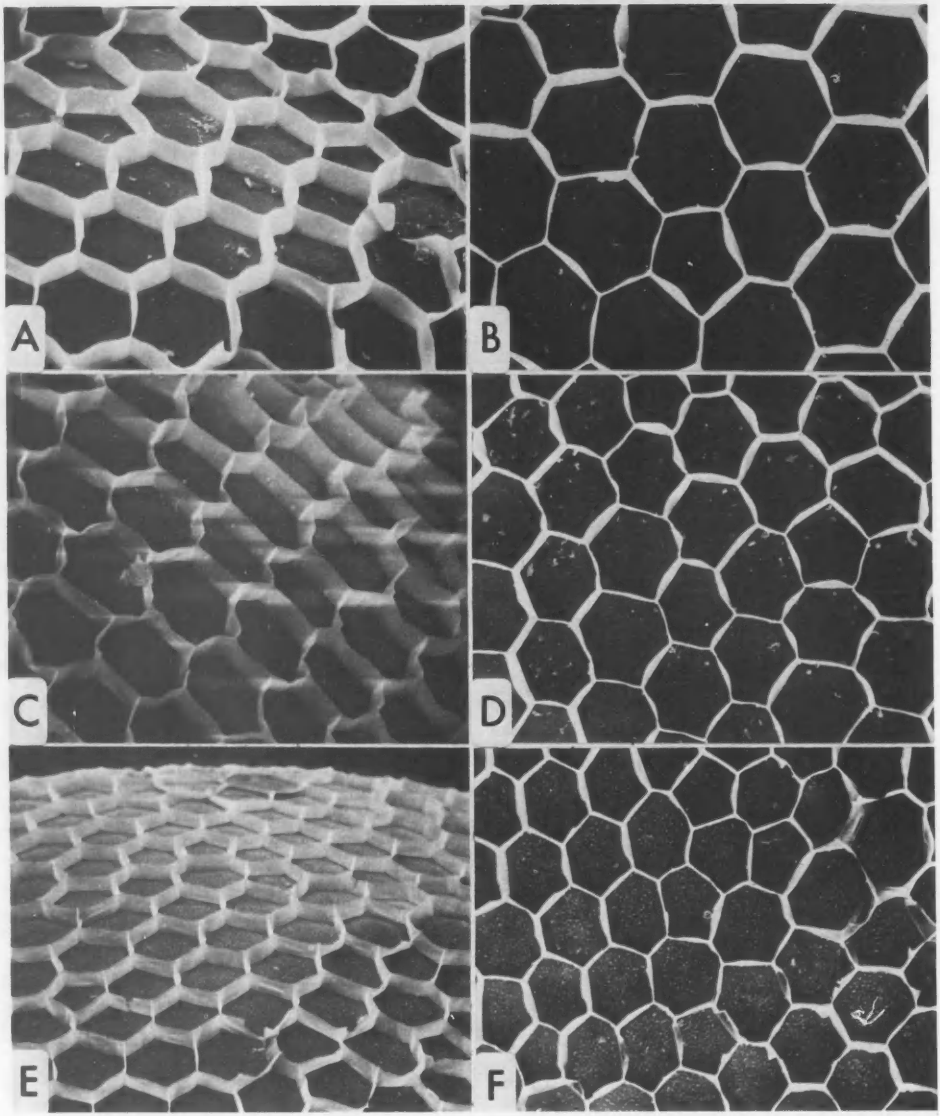


FIGURE 2.—Scanning electromicrographs of *Pleuronichthys* eggs. A. Side view of *P. decurrens* egg, 475×; B. Face view of same egg, 475×; C. Side view of *P. verticalis* egg, 410×; D. Face view of same egg, 450×; E. Side view of *P. ritteri* egg, 460×; F. Face view of same egg, 475×.

diameter (Table 2). There was no evidence of other small oil globules in the yolk, although a few eggs had a damaged oil globule which had separated in two. However, the original oil globule could easily be determined because of surrounding pigment. The oil globule is positioned near the center of the developing embryo in middle-stage eggs. The body of the late-stage embryo is heavily pigmented, similar to the newly hatched larvae.

Hippoglossina stomata

Eggs of *H. stomata* have not been previously described. Eggs are round with a slightly pinkish, unornamented shell and a single oil globule. The egg has a mean diameter of 1.29 mm (range 1.22-1.38 mm) and the oil globule a mean diameter of 0.23 mm (range 0.20-0.26 mm) (Table 2). The oil globule lacks pigment and lies near the tip of the tail of developing embryos in middle-stage eggs. In late-stage eggs the oil globule is in the posterior part of the yolk sac; the embryo is heavily pigmented over the body except for the posteriormost portion of the tail; pigment patches occur on the finfolds in the same places as in early preflexion stage larvae; pigment is widespread over the yolk surface.

DESCRIPTION OF DEVELOPMENTAL STAGES—LARVAL, TRANSFORMING, AND EARLY JUVENILE

Pleuronichthys decurrens Jordan and Gilbert (curlfin turbot) Figures 3, 4

Literature.—A series of egg stages and two preflexion larvae of *P. decurrens* were described and illustrated by Budd (1940) but incorrectly identified as *P. coenosus*. His larval illustrations were based on a recently hatched specimen, 5.54 mm, and an emaciated specimen, 8 days old, of somewhat smaller size.

Distinguishing characters.—Larvae of this species are unique in the genus *Pleuronichthys* in developing a pterotic spine on each side of the head, in having a higher precaudal vertebral number of 14 or 15, and in having the largest larvae during all stages of development. Larval pigmentation is heaviest in this species with the body and finfold entirely pigmented except for the posteriormost region. Because of their relatively large size and dense pigment, *P. decurrens* larvae cannot be confused with *Hippoglossina stomata* or *Hypsopsetta guttulata*.

Pigmentation.—Newly hatched, preflexion, and early flexion larvae (4.9-9.8 mm NL) are heavily pigmented over the head, trunk, tail, and finfolds with only the pectoral fin and posteriormost tip of the notochord and finfold unpigmented (Figure 3A, B, C). As the first few caudal rays become evident (ca. 9.7 mm NL), several small, discrete melanophores appear on the pectoral fin base (Figure 3C). In late flexion and early postflexion stages during dorsal and anal fin development, the continuous heavy pigment on the finfolds changes to form three to four dorsal and three ventral bands of pigment which extend out from the body margin to part of the rayed fin membrane (Figure 3D). Larvae at this stage have a soft, saccular body with semitransparent and sparsely pigmented areas in the pterygiophore region between the body proper and developing dorsal and anal fins. Larvae >11.2 mm SL have dorsal and anal pterygiophores fully developed; the pterygiophore region is no longer transparent and the specimens become robust (Figure 4).

Morphology.—Larvae of *P. decurrens* are the largest members of the genus at hatching and attain the largest size before transformation. Our smallest specimen is 4.9 mm NL and has yolk remnants (Table 4). The left eye begins to migrate at 10.5 mm SL and has not completed migration in a larva 21.0 mm SL. The smallest available juvenile is 29.4 mm SL.

The gut begins as a tube which diminishes in diameter posteriorly and ends with a free terminal section that diverges from the body in a slight posteriad direction. In 5- to 7-mm NL larvae, the gut increases markedly in diameter and the free terminal section becomes vertical to the body axis. At about 8.0 mm NL, the gut begins to coil and its terminal section begins to slant anteriad. Coiling and the anterior displacement of the anus become more marked as development proceeds. This is reflected in the decreasing relative snout-anus length in postflexion larvae and especially in juveniles (Table 5).

Relative head length increases during larval development whereas relative snout length decreases (Table 5). Relative eye width decreases slightly during the three phases of the larval

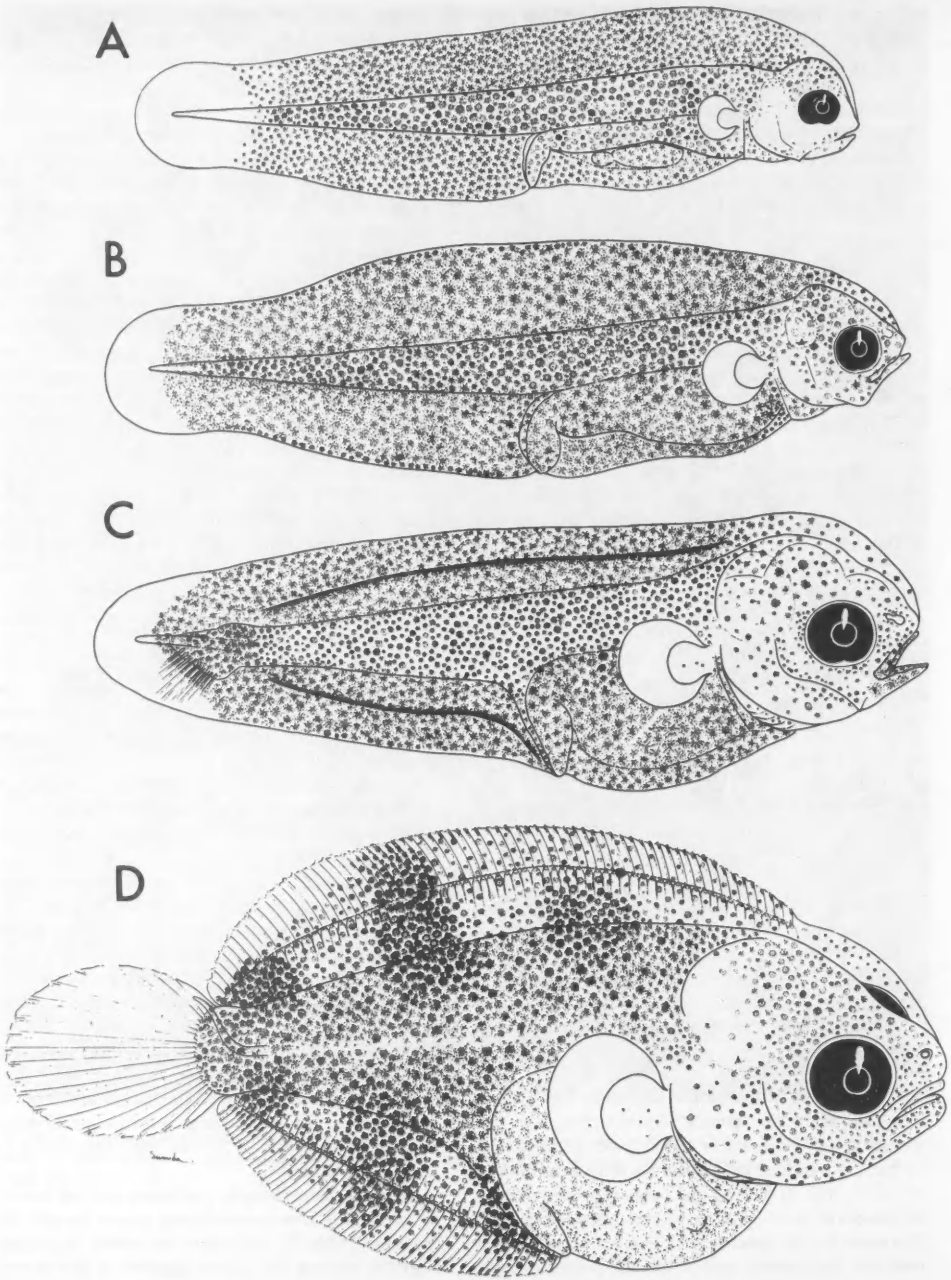

A
B
C
D

FIGURE 3.—Larval stages of *Pleuronichthys decurrens*: A. 5.9 mm; B. 6.5 mm; C. 9.7 mm; D. 10.0 mm.

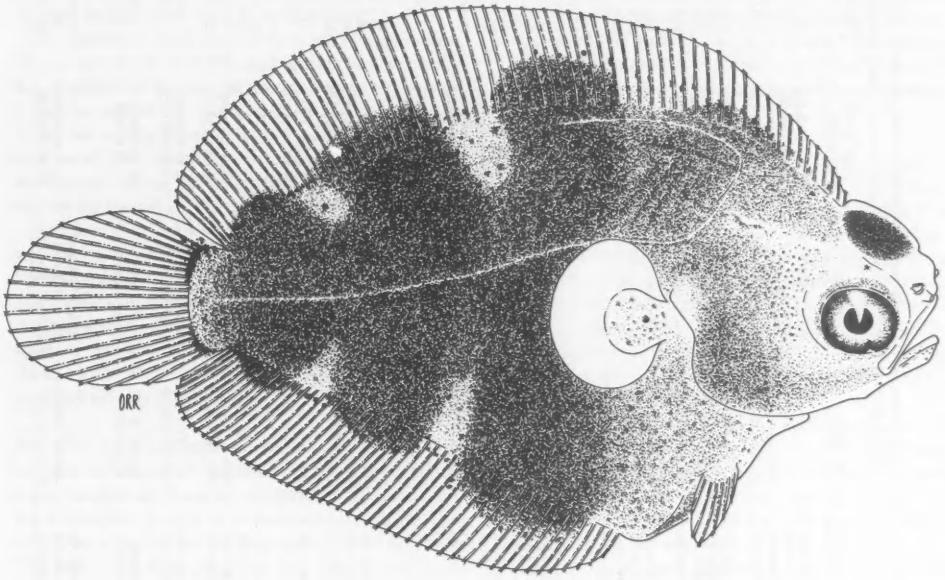


FIGURE 4.—Transforming specimen of *Pleuronichthys decurrens*, 14.4 mm.

TABLE 4.—Morphometrics, in millimeters, of larvae and a juvenile of *Pleuronichthys decurrens*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5401-90.60	4.9 NL	Sym.	Str.	2.4	0.80	0.14	0.30	0.24	0.54	0.64	—	—	—
5704-87.50	5.6	Sym.	Str.	3.0	1.1	0.20	0.40	0.32	0.90	0.96	—	—	—
6501-63.52	6.0	Sym.	Str.	3.0	1.1	0.20	0.40	0.36	0.90	0.74	—	—	—
5206-70.65	6.5	Sym.	Str.	3.2	1.2	0.22	0.42	0.40	0.94	1.1	—	—	—
6501-60.70	7.9	Sym.	Str.	3.9	1.6	0.30	0.50	0.48	1.3	1.3	—	—	—
5003-87.35	8.5	Sym.	Str.	4.1	1.8	0.32	0.60	0.56	1.7	1.8*	—	—	—
6606-60.65	9.3	Sym.	Str.	4.3	2.0	0.32	0.66	0.62	1.6	1.8*	—	—	—
6605-80.80	9.8	Sym.	Str.	4.3	2.2	0.36	0.68	0.64	2.0	2.2*	—	—	—
5706-93.65	7.8	Sym.	E fl.	3.9	1.9	0.30	0.64	0.64	2.3*	2.3*	—	—	—
5711-87.55	9.1	Sym.	E fl.	4.7	2.1	0.40	0.70	0.66	2.4*	2.5*	—	—	—
5401-85.60	10.0	Sym.	Midfl.	4.4	2.6	0.44	0.80	0.72	2.8*	3.0*	—	—	2.7
6507-87.55	11.0	Sym.	L fl.	5.8	3.2	0.48	0.98	1.0	4.0*	4.6*	—	—	3.3
5009-47.60	10.2 SL	Sym.	Flexed	5.3	3.4	0.60	0.96	0.94	4.5*	4.6*	1.0	0.60	3.4
5407-60.70	10.5	Migr.	Flexed	5.5	3.6	0.64	1.1	1.1	4.9*	5.4*	1.0	0.64	3.4
5805-70.80	11.2	Migr.	Flexed	5.7	3.9	0.64	1.3	1.2	5.2*	5.9*	1.3	0.68	3.6
7505-90.70	14.5	Migr.	Flexed	6.2	5.2	0.66	1.6	0.96	8.1*	8.6*	2.1	0.83	4.6
4903-82.57	15.4	Migr.	Flexed	7.0	5.7	0.67	1.8	1.7	9.0*	9.7*	2.1	1.1	4.7
6609-80.60	17.0	Migr.	Flexed	8.7	6.4	0.67	1.9	1.5	9.2*	11.4*	2.9	1.2	6.0
5308-73.60	19.2	Migr.	Flexed	7.7	6.5	0.91	1.7	1.5	10.0*	11.4*	2.8	1.2	6.4
5004-97.32	21.0	Migr.	Flexed	8.4	6.7	0.66	1.7	1.7	11.7*	12.4*	3.2	1.4	6.2
Off Santa Cruz Island, Calif.	29.4	Over	Juv.	9.7	9.0	0.66	3.3	2.5	13.9*	14.5*	3.6	2.2	6.8

[1]Sym. - symmetrical; Migr. - migrating.
[2]Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 5.—Body proportions of larvae and early juveniles of seven flatfishes with heavily pigmented larvae. (Values given for each body proportion expressed as percentage of body length or head length: mean, standard deviation, and range. Numbers derived from data in morphometric tables for each species.)

Body proportion	*Pleuronichthys decurrens*	*P. coenosus*	*P. verticalis*	*P. ocellatus*	*P. ritteri*	*Hypsopsetta guttulata*	*Hippoglossina stomata*
Snout to anus/body length:							
Preflexion	48.6±2.9(44-54)	46.2±3.4(39-50)	50.9±1.2(50-53)	—	49.2±3.8(44-57)	50.0±1.2(48-52)	40.1±3.9(36-45)
Flexion	49.8±4.0(44-53)	44.5±3.3(42-51)	50.0±4.7(44-56)	—	49.0±1.4(48-51)	48.5±1.7(46-50)	39.4±1.4(37-41)
Postflexion	46.9±5.3(40-52)	42.4±4.6(37-49)	42.7±4.3(36-45)	47.5±0.7(47-48)	40.7±7.9(31-51)	44.6±5.2(37-52)	40.5±2.6(36-44)
Juvenile	33	31	32.4±0.9(31-33)	32.2±2.2(30-36)	31.2±1.3(30-33)	36.0±1.1(35-38)	33.5±2.1(32-35)
Head length/body length:							
Preflexion	19.6±2.1(16-22)	20.0±2.7(15-23)	22.1±1.7(20-25)	—	24.4±2.3(20-28)	21.6±2.8(17-25)	21.5±3.3(17-26)
Flexion	25.5±2.6(23-29)	24.8±3.3(22-31)	27.3±1.9(25-30)	—	27.2±3.9(22-31)	25.8±1.3(24-27)	25.6±1.9(22-28)
Postflexion	34.9±2.0(32-38)	31.1±1.8(28-33)	33.2±2.6(31-37)	30.0	32.8±1.5(31-35)	33.0±1.9(30-36)	31.4±1.7(29-34)
Juvenile	31	28	27.4±1.5(26-30)	27.8±1.2(27-30)	29.0±1.2(28-30)	33.0±0.6(32-34)	34.5±0.7(34-35)
Snout length/head length:							
Preflexion	17.6±1.1(16-19)	20.5±3.5(16-27)	22.4±2.8(18-26)	—	18.8±1.8(17-22)	21.9±2.8(18-26)	18.1±4.0(10-24)
Flexion	16.8±1.7(15-19)	18.1±2.4(14-21)	19.7±3.1(15-23)	—	22.0±4.7(17-28)	18.8±1.5(17-20)	20.9±2.2(18-24)
Postflexion	13.9±3.2(10-18)	16.7±2.1(13-19)	14.7±2.9(11-18)	17.0±2.8(15-19)	16.3±1.4(15-18)	17.9±1.6(16-20)	23.1±2.8(19-27)
Juvenile	7	12	6.2±3.0(2-10)	14.2±1.5(12-16)	10.8±1.0(10-12)	14.7±1.8(12-17)	19.5±0.7(19-20)
Eye width/head length:							
Preflexion	34.1±2.5(31-38)	36.6±4.1(31-43)	36.4±4.1(31-44)	—	37.2±6.0(31-48)	40.6±3.1(37-45)	35.1±4.9(28-44)
Flexion	32.0±1.5(31-34)	32.0±2.6(28-35)	32.5±1.0(31-34)	—	33.5±6.4(29-43)	31.8±1.0(31-33)	31.9±1.5(30-34)
Postflexion	29.5±2.9(25-33)	29.6±1.7(26-31)	32.5±4.5(29-41)	28.5±2.1(27-30)	30.8±1.2(30-32)	31.5±2.7(28-36)	30.5±2.2(27-34)
Juvenile	37	30	38.4±3.0(34-42)	33.3±2.2(31-37)	36.2±2.9(32-38)	30.7±3.7(28-38)	33.0±2.8(31-35)
Eye height/head length:							
Preflexion	30.8±1.6(29-33)	32.1±2.0(29-35)	32.6±4.2(26-39)	—	32.8±3.9(29-40)	33.6±2.6(32-37)	28.6±3.4(26-33)
Flexion	31.0±2.4(28-34)	29.0±3.3(24-34)	30.8±1.7(28-33)	—	32.2±4.6(27-40)	28.8±1.5(27-30)	30.8±3.8(26-37)
Postflexion	26.1±4.7(18-31)	26.7±1.4(25-28)	27.0±2.8(23-30)	27.5±0.7(27-28)	27.2±2.3(25-31)	25.5±1.8(22-28)	29.4±3.7(24-36)
Juvenile	28	—	29.6±4.1(23-33)	33.3±2.2(31-37)	28.3±2.1(26-30)	24.2±3.4(21-30)	—
Body depth at P base before development of D base/body length:							
Preflexion	16.1±3.0(11-20)	17.4±4.5(8-22)	16.7±3.7(9-20)	—	20.9±6.4(10-28)	18.6±7.3(8-25)	17.6±4.5(12-23)
Flexion	—	23	—	—	—	23.2±1.0(22-24)	—
Body depth at P base after development of D base/body length:							
Preflexion	—	—	—	—	35	—	28.1±6.1(22-34)
Flexion	30.0±4.3(26-36)	27.4±4.0(22-33)	29.8±3.1(25-33)	—	33.8±2.6(31-36)	—	30.6±2.1(28-33)
Postflexion	51.6±5.3(44-58)	39.9±5.9(31-45)	39.7±5.0(31-46)	33.0	40.7±1.5(39-42)	39.2±6.2(33-47)	38.1±2.0(36-41)
Juvenile	47	45	40.4±0.9(39-41)	42.0±1.6(39-43)	39.5±2.1(37-42)	52.8±1.5(51-54)	37.0
Body depth at anus before development of D&A bases/body length:							
Preflexion	15.0±2.4(12-17)	15.7±2.9(12-19)	14.3±0.8(13-15)	—	18.0±2.4(14-20)	18.4±3.4(13-22)	14.6±3.9(9-21)
Flexion	—	—	—	—	—	22.2±0.5(22-23)	—
Body depth at anus after development of D&A bases/body length:							
Preflexion	20.7±1.5(19-22)	—	—	—	27.7±5.5(22-33)	—	26
Flexion	32.5±6.4(28-42)	28.3±4.2(24-35)	27.7±4.1(21-32)	—	33.2±4.4(27-36)	—	26.6±2.6(24-31)
Postflexion	57.0±7.0(45-67)	44.1±7.1(32-50)	41.7±5.8(31-46)	33.0	42.2±1.6(40-45)	41.2±6.1(35-48)	38.0±4.4(33-45)
Juvenile	49	49	42.2±0.8(41-43)	44.8±1.7(42-47)	40.8±1.9(38-42)	54.7±1.2(54-57)	36.0
Caudal peduncle depth/body length:							
Postflexion	13.4±2.5(10-17)	12.4±2.4(9-16)	11.8±1.9(8-13)	7.5±0.7(7-8)	12.0±1.8(9-14)	9.1±1.4(8-11)	8.9±0.8(8-10)
Juvenile	12	14	13.2±0.8(12-14)	12.5±0.6(12-13)	11.5±0.6(11-12)	11.5±0.6(11-12)	9.5±0.7(9-10)
Caudal peduncle length/body length:							
Postflexion	6.4±0.5(6-7)	5.1±0.4(5-6)	6.5±1.2(5-8)	6.5±0.7(6-7)	5.8±0.8(5-7)	8.5±0.5(8-9)	8.5±0.5(8-9)
Juvenile	7	6	6.6±0.6(6-7)	6.3±0.5(6-7)	6.2±1.0(5-7)	8.0±1.1(6-9)	8.5±0.7(8-9)
Snout to pelvic base/body length:							
Preflexion	—	—	—	—	26	—	—
Flexion	28.5±2.1(27-30)	22.8±2.4(20-27)	26.2±1.8(25-29)	—	27.5±1.9(25-29)	—	24.4±1.8(22-27)
Postflexion	32.1±1.6(30-35)	28.6±0.8(28-30)	28.6±3.1(24-32)	29.5±0.7(29-30)	29.3±3.9(26-36)	29.8±1.9(26-32)	28.0±2.6(24-30)
Juvenile	23	22	24.4±1.1(23-26)	23.8±1.3(22-26)	25.0±2.2(22-27)	27.8±0.8(27-29)	29.5±0.7(29-30)

period and then increases sharply in juveniles (Table 5). Relative eye height is consistently less than eye width; this is the usual pattern among all species being dealt with in this report.

The spine on each pterotic bone first appears on larvae about 6.0 mm NL and achieves maximum development in flexion larvae. It begins to regress near the end of the larval period and is a rugose bump in newly transformed juveniles. No other species of *Pleuronichthys* develops pterotic spines during the larval period, although they are present on larvae of *H. guttulata*.

Another distinctive feature of *P. decurrens* larvae is body depth. As in other species of *Pleuronichthys*, early larvae are slender. Relative body depth increases markedly during the postflexion stage with the result that larvae of this species become strikingly deeper bodied than those of the other six flatfishes with heavily pigmented larvae (Table 5).

Fin and axial skeleton formation.—Because this species is larger at corresponding stages of development than the other six flatfishes considered, fin formation occurs at comparatively larger larval sizes. Caudal fin development occurs between 7.9 and 11.0 mm NL; the smallest postflexion specimen, 10.2 mm SL, has the full count of 19 caudal rays (Table 6). The dorsal and anal fins begin forming simultaneously with the caudal, but obtain their full complement of rays later, by 14.5 mm SL. Pelvic buds are evident on most specimens undergoing flexion, but the full count of fin rays was first obtained on a 15.4-mm SL specimen. The axial skelton is ossified on specimens as small as 11.2 mm SL, as determined by radiographs. Counts of 14 precaudal and 24-27 caudal vertebrae were recorded on five postflexion specimens.

Transformation.—Flatfish larvae are normally symmetrical larvae with eyes opposite each other on either side of the head during their preflexion to flexion stages and into the postflexion stage. Some flatfish larvae remain symmetrical with regard to eye placement until attaining quite large sizes, i.e., 50-120 mm (Hubbs and Chu 1934; Bruun 1937; Nielsen 1963; Amaoka 1970, 1971, 1972, 1973). However, in the flatfishes being studied the migration of one eye (left in dextral flounders, right in sinistral flounders) begins early in the postflexion stage. It can require some time to move completely over. Thus, the left eye was migrating on a 10.5-mm larva of *P. decurrens*, but was not completely over on a 21.0-mm specimen. Ossified rays are not formed in the pectoral fin until after eye migration is completed. On first formation the rays are spaced some distance apart in the blade of the pectoral fin. The pectoral fin rapidly changes form with the structure of the larval pectoral (base and blade) disappearing, to be replaced by a group of ossified, closely spaced rays. Metamorphosis is

TABLE 6.—Meristics of larvae and a juvenile of *Pleuronichthys decurrens*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5401-90.60	4.9 NL	Prefl.	0	0	0	0	LP[2]				
5704-87.50	5.6	Prefl.	0	0	0	0	LP[2]				
6501-63.52	6.0	Prefl.	0	0	0	0	LP[2]				
5206-70.65	6.5	Prefl.	0	0	0	0	LP[2]				
6501-60.70	7.9	Prefl.	0	0	0	0	LP[2]				
5003-87.35	8.5	Prefl.	Forming	Forming	Forming	0	LP[2]				
6606-60.65	9.3	Prefl.	Forming	Forming	4	0	LP[2]				
6605-80.80	9.8	Prefl.	Forming	Forming	ca. 8	0	LP[2]				
5706-93.65	7.8	E fl.	Forming	Forming	ca. 8	Bud	LP[2]				
5711-87.55	9.1	E fl.	Forming	Forming	ca. 12	0	LP[2]				
5401-85.60	10.0	Midfl.	Forming	Forming	ca. 12	Bud	LP[2]				
6507-87.55	11.0	L fl.	ca. 50	ca. 42	17	Bud	LP[2]				
5009-47.60	10.2 SL	Postfl.	>50	46	19	Bud	LP[2]				
5407-60.70	10.5	Postfl.	ca. 64	45	19	5/5	LP[2]				
5805-70.80	11.2	Postfl.	71	46	19	5/5	LP[2]	14	25	39	X-ray
7505-90.70	14.5	Postfl.	74	52	19	5/5	LP[2]				
4903-82.57	15.4	Postfl.	72	48	19	6/6	LP[2]	14	25	39	X-ray
6609-80.60	17.0	Postfl.	77	48	19	6/6	LP[2]	14	24	38	X-ray
5308-73.60	19.2	Postfl.	75	52	19	6/6	LP[2]	14	27	41	X-ray
5004-97.32	21.0	Postfl.	74	48	19	6/6	LP[2]	14	25	39	X-ray
Off Santa Cruz Island, Calif.	29.4	Juv.	78	52	19	6/6	11/11	14	26	40	X-ray

[1]Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

considered complete when the lateral line can be discerned and scale formation has begun.

Distribution.—Fitch (1963) reported that the range for this species was from Alaska to San Quintin, Baja California. Miller and Lea (1976) gave an extended southern range limit to 25 mi north-northeast of Cedros Island (lat. 28°47.5'N, long. 114°57.0'W). Egg and larval material in our collections was taken off the entire coast of California over a broad band of stations, from nearshore to 150 or more miles offshore (Figure 5). Lack of egg and larval material off Baja California, despite the intensive coverage of these waters by CalCOFI surveys, indicates a more northerly distribution for young stages than for adults.

Pleuronichthys coenosus Girard
(C-O turbot)
Figures 6, 7

Literature.—Budd (1940) described and illustrated a series of eggs and four reared larvae of *P. coenosus* which he mistakenly identified as *P. decurrens*. The larvae illustrated were newly hatched to 9 days old, ranging in size from 3.88 to 4.72 mm.

Distinguishing characters.—This species is distinguished by having 13 (rarely 12) precaudal vertebrae and a total of 37-39 vertebrae. The larvae are larger than comparable stages of *H. guttulata* and other species of *Pleuronichthys* except *P. decurrens*. Pigmentation patterns discussed below will also separate *P. coenosus* from other species treated in this work.

Pigmentation.—Preflexion larvae are characterized by having opposing, similar appearing, pigment clusters on the dorsal and ventral finfolds posterior to the anus, and by small melanophores dotting the margin of the otherwise unpigmented posterior tip of the tail (Figure 6A, B). The rest of the body is heavily pigmented, with the exclusion of the undifferentiated pectoral fin and the ventral half of the head.

Flexion (6.2-7.8 mm NL) and postflexion larvae (7.1-11.4 mm SL) show an increase anteriorly of the finfold pigment and an increase in pigmentation on the lower region of the head (Figure 6C, D, E). A distinctively narrow, unpigmented zone along the hypurals persists through late flexion specimens, but is subsequently pigmented in

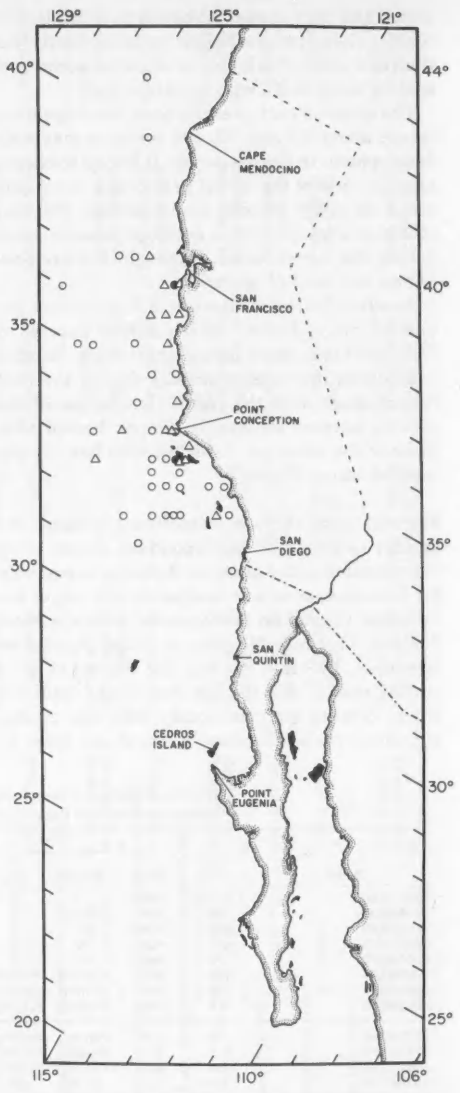
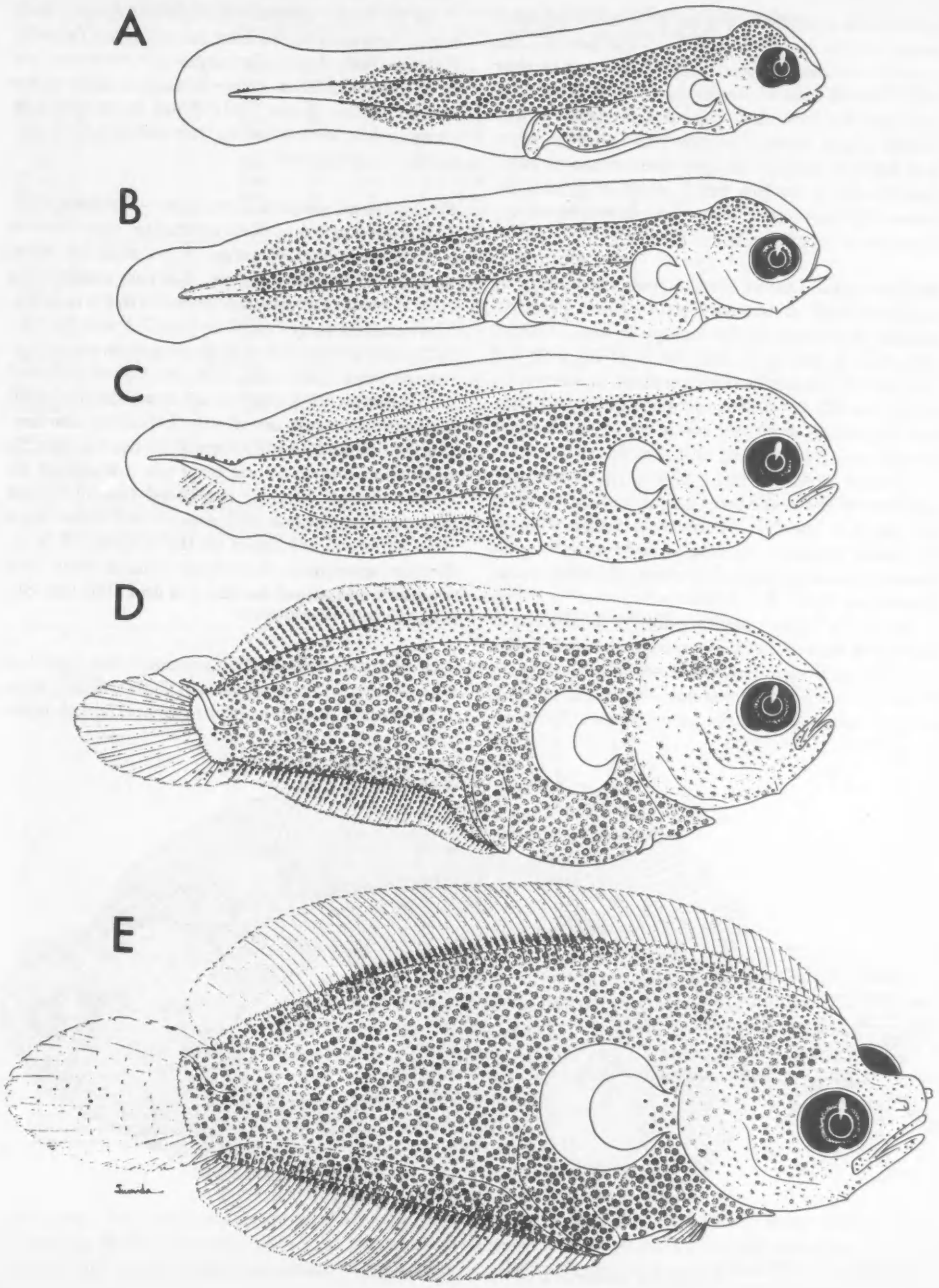


FIGURE 5.—Distribution of eggs and larvae of *Pleuronichthys decurrens* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

FIGURE 6.—Larval stages of *Pleuronichthys coenosus*: A. 3.7 mm; B. 5.9 mm; C. 6.1 mm; D. 7.8 mm; E. 8.9 mm.


A
B
C
D
E

postflexion specimens (Figure 6E). A few pigment spots dot the anterior margin of the pectoral fin base in postflexion specimens, and extend farther onto the fin base in larger specimens. At dorsal and anal fin formation, pigment clustered in the finfold aligns along the dorsal and anal fin rays, and later in postflexion specimens becomes compacted into a narrow band adjacent to the fin bases. Pigment over the pterygiophores, however, is as dense as on the body (Figure 7).

Morphology.—Larvae of *P. coenosus* are larger at hatching and at transformation than all other species of *Pleuronichthys* except *P. decurrens*. A 3.9-mm NL specimen has much of its yolk sac remaining (Table 7). The smallest specimen in which the left eye begins to migrate is 8.2 mm SL; eye migration is almost complete in our largest transforming specimen, 11.4 mm SL.

The gut begins to coil and the free section becomes vertical to the body axis in larvae between 5.5 and 6.0 mm NL. Snout-anus distance has a moderate decrease relative to body length in all larval phases and decreases markedly after transformation (Table 5).

As in the other species, relative head length increases during larval development through the postflexion stage, but decreases moderately in juveniles. Both relative snout length and eye size decrease during the three larval phases (Table 5).

As in other species of *Pleuronichthys*, body depth increases during each larval stage (Table 5). Relative body depths for larvae of *P. coenosus* are in the intermediate range compared with other species in the genus. Body depth in juveniles is comparable with that in the relatively deep-bodied *P. decurrens*.

Fin and axial skeleton formation.—Fin formation in *P. coenosus* takes place at smaller sizes than in *P. decurrens* but at larger sizes than in other species of *Pleuronichthys*. Larvae undergoing caudal fin formation range from 6.2 to 8.5 mm NL. The smallest fully flexed larva is 7.1 mm SL. The full count of caudal rays is developed on a postflexion specimen 8.2 mm SL (Table 8). Dorsal and anal fin formation takes place at the same size as caudal fin formation; rays are mostly formed on late flexion specimens and fully formed on the 8.2-mm SL postflexion larva. Pelvic buds are present on all specimens undergoing notochord flexion except the smallest (6.2 mm NL), and the full count of six rays per fin is developed on the 9.6-mm SL postflexion specimen. Vertebral counts from two cleared and stained larvae, 8.6 and 10.0 mm SL, are 13+24.

Distribution.—Fitch (1963) denoted the distribution of *P. coenosus* as Alaska to Cape Colnett, Baja California. Collections of our egg and larval mate-

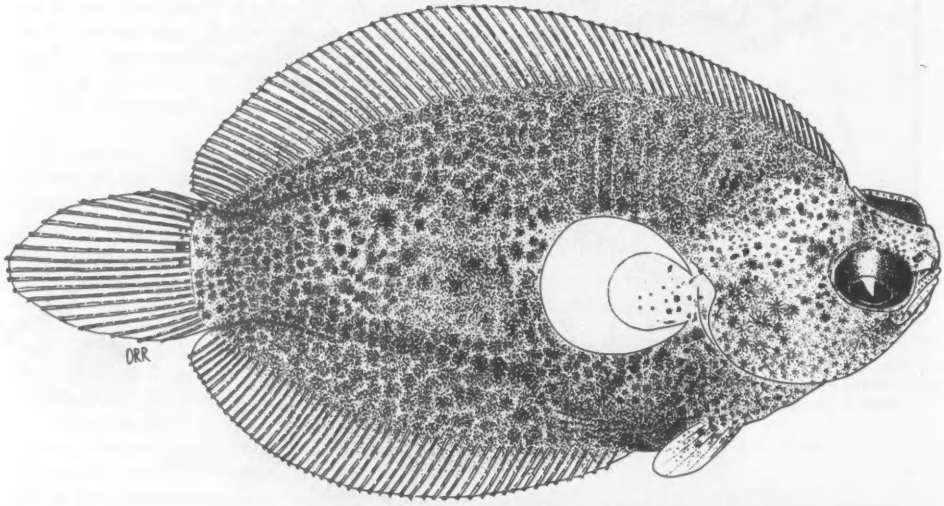


FIGURE 7.—Transforming specimen of *Pleuronichthys coenosus*, 10.0 mm.

TABLE 7.—Morphometrics, in millimeters, of larvae and a juvenile of *Pleuronichthys coenosus*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5902-83.43	3.9 NL	Sym.	Str.	1.8	0.60	0.16	0.26	0.20	0.30	0.46	—	—	—
5007-127.50	3.7	Sym.	Str.	1.8	0.68	0.14	0.26	0.22	0.60	0.52	—	—	—
5005-120.45	4.2	Sym.	Str.	2.1	0.80	0.16	0.32	0.24	0.70	0.56	—	—	—
Off La Jolla, Calif.	5.1	Sym.	Str.	2.5	1.1	0.20	0.40	0.38	1.1	0.90	—	—	—
5704-82.47	5.6	Sym.	Str.	2.6	1.1	0.26	0.40	0.36	0.90	0.84	—	—	—
6304-93.40	6.9	Sym.	Str.	3.1	1.6	0.30	0.50	0.46	1.3	1.3	—	—	—
6304-120.70	6.5	Sym.	Str.	3.0	1.5	0.28	0.46	0.46	1.4	1.6*	—	—	—
5206-90.41	8.5	Sym.	Str.	3.3	1.7	0.28	0.64	0.60	1.6	1.6	—	—	—
5110-97.30	6.2	Sym.	E fl.	2.7	1.4	0.30	0.48	0.42	1.4	1.5*	—	—	—
7207-93.45	7.2	Sym.	E fl.	3.1	1.6	0.30	0.56	0.54	1.6	1.8*	—	—	1.6
5705-93.27	7.4	Sym.	Midfl.	3.3	1.8	0.26	0.60	0.54	2.0*	1.9*	—	—	1.6
5304-85.50	8.3	Sym.	Midfl.	3.5	1.9	0.36	0.60	0.54	2.2*	2.4*	—	—	1.7
1941-25.45	7.2	Sym.	L fl.	3.1	1.9	0.36	0.58	0.54	2.1*	2.2*	—	—	1.6
4908-72.56	7.8	Sym.	L fl.	4.0	2.4	0.40	0.68	0.58	2.6*	2.7*	—	—	2.1
5007-90.53	7.1 SL	Sym.	Flexed	3.3	2.0	0.38	0.62	0.56	2.2*	2.3*	0.62	0.36	2.0
5004-100.60	8.2	Migr.	Flexed	3.4	2.5	0.40	0.74	0.70	3.1*	3.4*	0.98	0.50	2.3
6606-70.70	8.8	Migr.	Flexed	4.0	2.7	0.48	0.80	0.74	2.9*	3.3*	0.84	0.42	2.6
5304-85.50	9.6	Migr.	Flexed	4.7	3.0	0.60	0.92	0.80	4.2*	4.8*	1.2	0.52	2.8
5206-90.41	9.9	A. over	Flexed	3.9	3.2	0.56	0.84	0.80	4.4*	4.9*	1.4	0.48	2.8
5407-83.51	10.2	A. over	Flexed	3.8	3.4	0.52	1.0	0.84	4.6*	5.1*	1.6	0.52	3.0
5304-100.29	11.4	Over	Flexed	4.3	3.4	0.60	1.0	0.88	5.0*	5.4*	1.6	0.60	3.2
Off Coronados Islands, B.C.	17.0	Over	Juv.	5.2	4.7	0.58	1.4	—	7.9*	8.3*	2.4	1.0	3.8

[1]Sym. - symmetrical; Migr. - migrating; A. over - About over.
[2]Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 8.—Meristics of larvae and a juvenile of *Pleuronichthys coenosus*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5902-83.43	3.9 NL	Yolk-sac	0	0	0	0	LP[2]				
5007-127.50	3.7	Prefl.	0	0	0	0	LP[2]				
5005-120.45	4.2	Prefl.	0	0	0	0	LP[2]				
Off La Jolla, Calif.	5.1	Prefl.	0	0	0	0	LP[2]				
5704-82.47	5.6	Prefl.	0	0	0	0	LP[2]				
6304-93.40	6.9	Prefl.	0	0	0	0	LP[2]				
6304-120.70	6.5	Prefl.	Forming	Forming	4	0	LP[2]				
5206-90.41	8.5	Prefl.	Forming	Forming	ca. 8	0	LP[2]				
5110-97.30	6.2	E fl.	Forming	Forming	ca. 8	0	LP[2]				
7207-93.45	7.2	E fl.	Forming	Forming	12	Bud	LP[2]				
5705-93.27	7.4	Midfl.	Forming	Forming	12	Bud	LP[2]				
5304-85.50	8.3	Midfl.	Forming	30	12	Bud	LP[2]				
1941-25.45	7.2	L fl.	ca. 55	ca. 44	ca. 14	Bud	LP[2]				
4908-72.56	7.8	L fl.	ca. 60	ca. 45	16	Bud	LP[2]				
5007-90.53	7.1 SL	Postfl.	ca. 70	ca. 50	16	Bud	LP[2]				
5004-100.60	8.2	Postfl.	74	55	19	ca. 4/4	LP[2]				
6606-77.55	8.6	Postfl.	72	54	19	ca. 5/5	LP[2]	13	24	37	C&S[3]
6606-70.70	8.8	Postfl.	76	50	19	ca. 4/4	LP[2]				
5304-85.50	9.6	Postfl.	73	ca. 52	19	6/6	LP[2]				
5206-90.41	9.9	Postfl.	69	50	19	6/6	LP[2]				
5206-87.45	10.0	Postfl.	71	53	19	—	LP[2]	13	24	37	C&S[3]
5407-83.51	10.2	Postfl.	69	49	19	6/6	LP[2]				
5304-100.29	11.4	Postfl.	72	50	19	6/6	LP[2]				
Off Coronados Islands, B.C.	17.0	Juv.	75	53	19	6/6	9/9	13	25	38	X-ray

[1]Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Post fl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.
[3]Cleared and stained.

rial range from northern California south to Point Abreojos, Baja California (Figure 8). Our records extend the range considerably southward for the species. Larval specimens range widely from nearshore to about 200 mi offshore, but most occurrences are between 50 and 200 mi offshore.

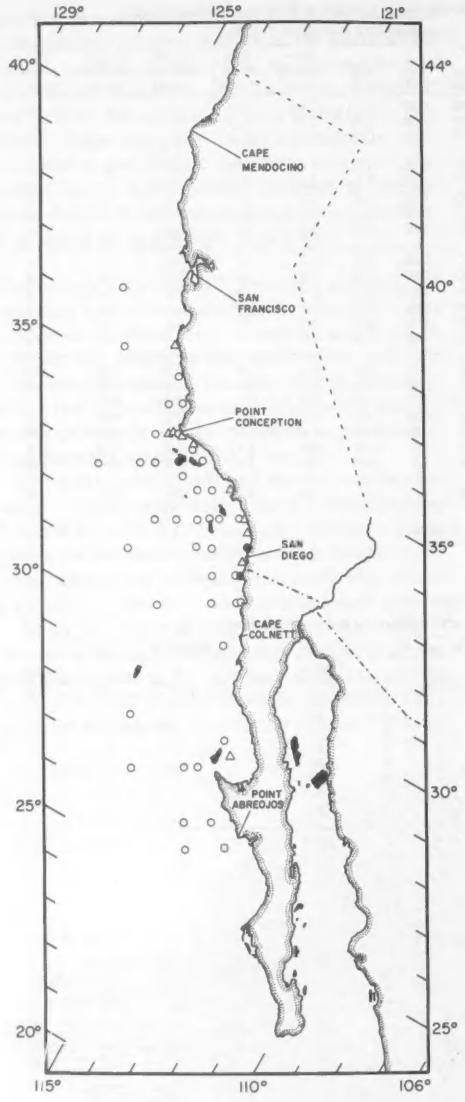


FIGURE 8.—Distribution of eggs and larvae of *Pleuronichthys coenosus* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

Pleuronichthys verticalis Jordan and Gilbert (hornyhead turbot) Figures 9, 10

Literature.—The eggs and two early larvae (3.16 and 3.35 mm) were described and illustrated by Budd (1940). Four illustrations of larvae, between 4.4 and 8.7 mm SL, are contained in CalCOFI Atlas No. 23 (Ahlstrom and Moser 1975).

Distinguishing characters.—Preflexion and early flexion larvae of this species are recognizable by the triangular patches of pigment, one each on the dorsal and ventral finfold posterior to the anus; these form late in the yolk-sac stage and persist through the notochord flexion stage. No other species of *Pleuronichthys* develops this distinctive pigmentation character.

Late flexion and postflexion larvae are distinguished by size (i.e., larger than *H. guttulata*, *P. ritteri*, and *P. ocellatus*, but smaller than *P. coenosus* and *P. decurrens*), and by sparse pigment on the head and on the dorsal and anal fin pterygiophores. This is in sharp contrast to the heavy pigment in these areas for the other species discussed.

Newly transformed specimens are difficult to distinguish from comparable stages of *P. ritteri*. However, pigment on the body tends to be mottled on *P. verticalis* rather than evenly distributed as on *P. ritteri* at this stage. Small juveniles are easily separable from *P. ritteri* because *P. verticalis* lacks the anterior prolongation of the supratemporal branch of the lateral line found on *P. ritteri* juveniles.

Pigmentation.—Pigment on yolk-sac and older preflexion larvae of *P. verticalis* is heavy on the head, trunk, and tail and ends anterior to the last three to five myomeres (Figure 9A, B). As the last remnant of yolk is absorbed, scattered finfold pigment differentiates into triangular-shaped clusters posterior to the anus, the dorsal patch being situated slightly anterior of the ventral patch. The head region below and on each side of the eye is only sparsely pigmented which is typical of most early preflexion larvae of several species of *Pleuronichthys*. The top of the head to the shoulder region is unpigmented, a character shared with preflexion larvae of *P. ritteri*. Small pigment spots dot the margin of the tip of the tail, but do not persist beyond the flexion stage (Figure 9C, D).

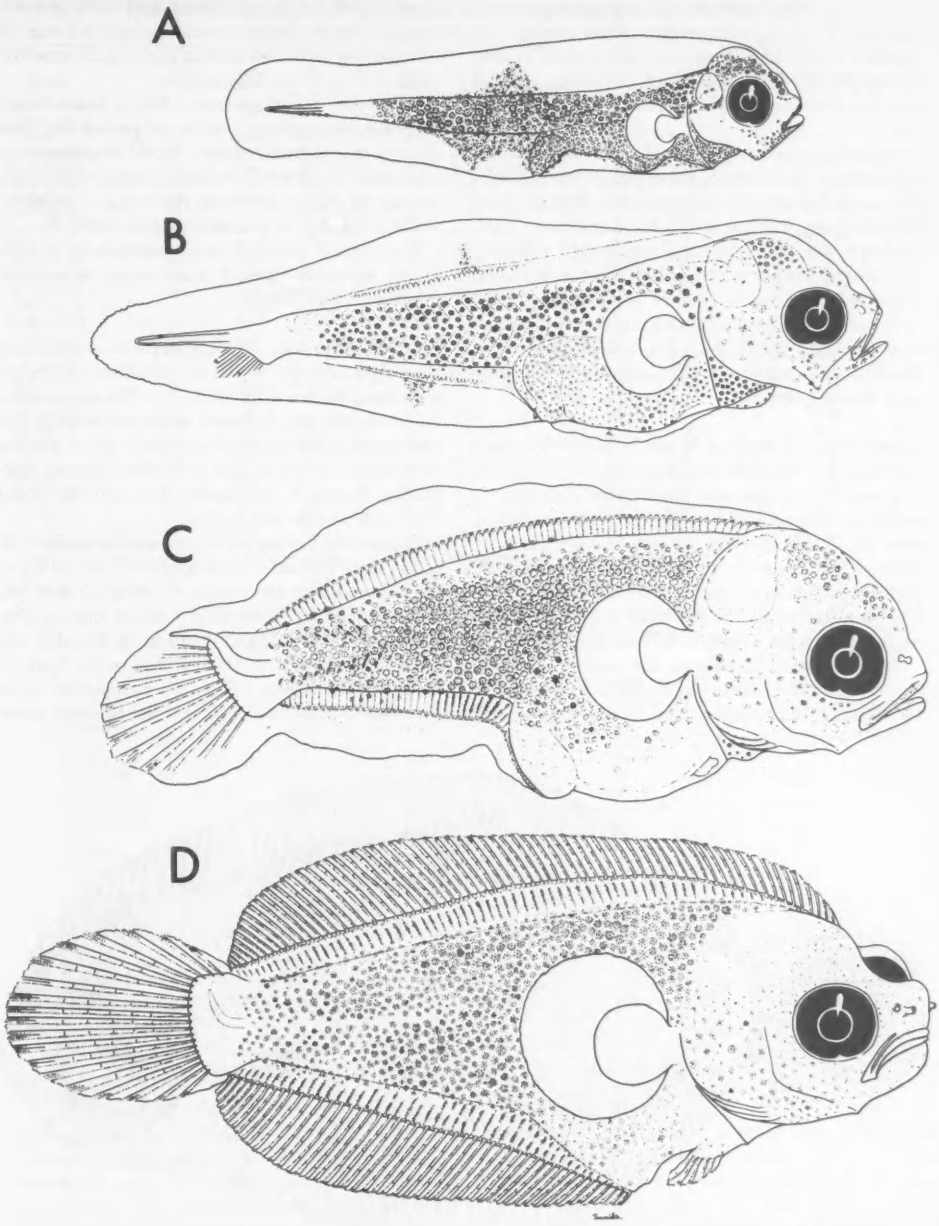


FIGURE 9.—Larval stages of *Pleuronichthys verticalis*: A. 4.4 mm; B. 6.5 mm; C. 7.1 mm; D. 8.7 mm.

Flexion larvae undergo little change in pigment pattern from earlier stages. The triangular patches of finfold pigment are diminished in size and pigment intensity, but are visible by careful examination in specimens through notochord flexion.

Following the completion of notochord flexion, pigment on the tail spreads posteriad leaving only the caudal peduncle unpigmented (Figure 9D). The outlying regions of the head and body, particularly the pterygiophore region, are sparsely pigmented compared with late larvae of other *Pleuronichthys* species and *H. guttulata*.

Transformed specimens develop heavy pigment over the body giving them a mottled appearance. Dark blotches appear along bases of the dorsal and anal fins (Figure 10).

Morphology.—Larvae of *P. verticalis* attain a size intermediate between the large species, *P. decurrens* and *P. coenosus*, and the smaller *P. ritteri*. A specimen with most of its yolk sac remaining is 2.4 mm NL (Table 9). The left eye is beginning to migrate in a specimen as small as 7.3 mm SL and transformation is almost complete at 9.2 mm SL. The smallest available juvenile is 12.2 mm SL, reared from eggs collected off San Diego, Calif.

Gut development follows the course of other *Pleuronichthys*. Snout-anus length is about 50% of body length in preflexion and flexion stages and then is reduced in postflexion and early juvenile stages. The gut begins to coil at about 4.0 mm NL but the free terminal section does not become vertical until at least 5.0 mm NL.

As in the other species, relative head length increases throughout the larval period and then decreases at transformation. Snout length and eye size undergo a gradual relative diminution during the larval stages; however, relative eye width increases sharply at transformation (Table 5).

Larvae of *P. verticalis* are intermediate in body depth when compared with other species of *Pleuronichthys* (Table 5).

Fin and structural development.—*P. verticalis* is the only species for which we could clear and stain a series of larvae (Tables 10, 11). The sequence of fin formation was followed more precisely in this species as was the sequence of ossification of other structures including the vertebral column, supporting bones of the caudal fin, branchiostegal rays, gill rakers, and teeth.

The caudal fin begins to form on the under side of the body a short distance anterior to the tip of the notochord on specimens of about 5.0 mm NL. Some caudal rays form before flexion begins (Figure 11A). Rays initially form at midcaudal and those that will be associated with superior hypural bones differentiate posteriorward, while those that will be associated with inferior hypural bones

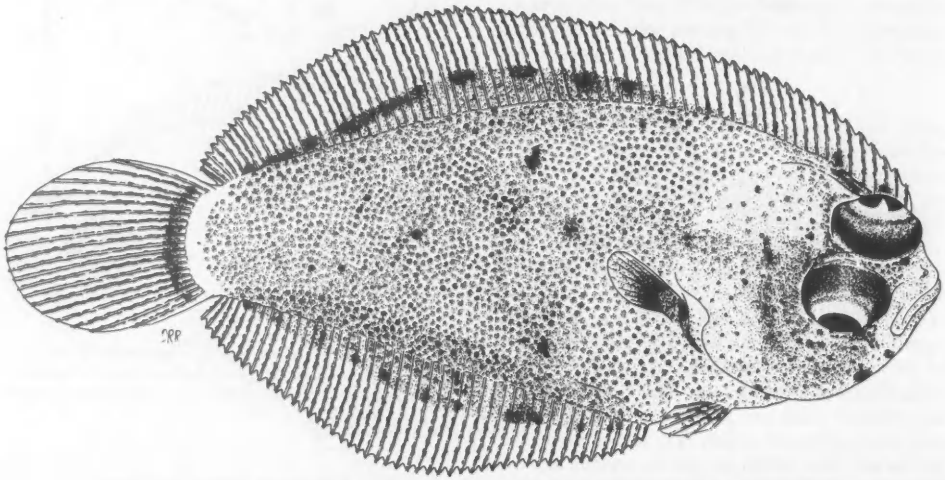


FIGURE 10.—Reared transforming specimen of *Pleuronichthys verticalis*, 11.0 mm.

TABLE 9.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys verticalis*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
7501-120.26 Off La Jolla, Calif.	2.4 NL	Sym.	Str.	1.2	0.56	0.10	0.22	0.20	0.22	0.34	—	—	—
SCBS-2-203	2.7	Sym.	Str.	1.4	0.54	0.12	0.24	0.22	0.38	0.40	—	—	—
7203-103.30	3.0	Sym.	Str.	1.5	0.64	0.16	0.22	0.20	0.48	0.40	—	—	—
7203-103.30	3.8	Sym.	Str.	2.0	0.86	0.20	0.30	0.26	0.70	0.54	—	—	—
7203-103.30	4.3	Sym.	Str.	2.2	0.94	0.24	0.34	0.32	0.84	0.62	—	—	—
7203-103.30	4.8	Sym.	Str.	2.4	1.0	0.20	0.36	0.32	0.90	0.70	—	—	—
7501-120.26	5.2	Sym.	Str.	2.6	1.3	0.30	0.40	0.34	1.0	0.80	—	—	—
5708-110.33	5.0	Sym.	E fl.	2.8	1.5	0.34	0.50	0.42	1.6*	1.4*	—	—	—
7203-103.30	5.6	Sym.	E fl.	2.7	1.4	0.30	0.48	0.46	1.4*	1.2*	—	—	1.5
7503-90.27.6	5.6	Sym.	Midfl.	2.9	1.5	0.30	0.48	0.46	1.8*	1.8*	—	—	1.4
5510-117.26	5.9	Sym.	Midfl.	2.7	1.6	0.24	0.50	0.52	1.7*	1.6*	—	—	1.5
7503-120.26	7.2	Sym.	Midfl.	3.2	1.9	0.32	0.60	0.56	2.1*	2.0*	—	—	1.8
5708-110.33	6.3	Sym.	L fl.	3.2	1.9	0.32	0.60	0.56	2.1*	2.0*	—	—	1.8
7505-120.30	6.5 SL	Sym.	Flexed	3.2	2.0	0.36	0.64	0.60	2.0*	2.0*	0.54	0.50	?
SCBS-4-303	7.3	Migr.	Flexed	3.3	2.6	0.40	0.76	0.68	3.1*	3.3*	0.96	0.40	2.2
5506-120.45	7.9	Migr.	Flexed	3.3	2.9	0.40	0.84	0.68	3.6*	3.6*	1.0	0.44	2.4
6606-103.29	8.3	Migr.	Flexed	3.5	2.7	0.48	0.84	0.68	3.2*	3.5*	1.0	0.44	2.7
6504-137.30	9.2	Migr.	Flexed	3.9	2.9	0.36	0.96	0.84	3.8*	4.2*	1.1	0.60	2.5
Reared	11.0	Over	Flexed	4.0	3.4	0.36	1.4	1.0	4.3*	4.4*	1.4	0.76	2.7
Reared	12.2	Over	Juv.	4.0	3.6	0.36	1.4	1.2	5.0*	5.1*	1.6	0.80	3.2
Reared	15.9	Over	Juv.	5.2	4.3	0.32	1.8	1.4	6.5*	6.6*	2.2	1.0	3.6
Reared	16.9	Over	Juv.	5.3	4.5	0.32	1.8	1.3	6.6*	6.9*	2.3	1.0	4.2
Santo Tomas Bay, B.C.	19.5 26.5	Over	Juv.	6.4 8.4	5.3 7.0	0.08 0.33	1.8 2.6	1.2 2.1	7.8* 10.9*	8.4* 11.4*	2.5 3.3	1.3 1.9	4.7 6.5

[1]Sym. - symmetrical, Migr. - migrating.
[2]Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 10.—Meristics of larvae and juveniles of *Pleuronichthys verticalis*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin ray					Gill rakers	Teeth			
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left		Upper jaw R	Upper jaw L	Lower jaw R	Lower jaw L
6609-97.29	5.3 NL	Prefl.	Forming	Forming	4	0	LP[2]	—				
7503-90.27.6	5.6	Prefl.	Forming	Forming	4	0	LP[2]	—				
—	5.5	Prefl.	Forming	Forming	6	0	LP[2]	—				
6507-107.30	5.8	Prefl.	Forming	Forming	6	0	LP[2]	—				
5708-117.26	5.7	Prefl.	Forming	Forming	6	0	LP[2]	—				
5708-117.26	5.8	Prefl.	Forming	Forming	6	0	LP[2]	—				
5708-117.26	6.1	E fl.	Forming	Forming	8	Bud	LP[2]	—				
—	7.0	L fl.	43	37	16	Bud	LP[2]	0+2	1	2	3	3
6606-97.29	6.9	L fl.	63	43	18	4/4	LP[2]	0+3	1	2	0	3
—	7.0	Postfl.	67	47	19	5/5	LP[2]	0+6	1	3	3	5
6407-83.43	7.1	Postfl.	64	44	19	3/3	LP[2]	Not taken	1	4	3	5
5110-100.40	7.3	Postfl.	67	47	19	5/5	LP[2]	0+5	?	6	5	6
6606-97.29	8.3	Postfl.	65	46	19	6/6	LP[2]	0+5	0	5	5	7
6504-137.30	9.2	Postfl.	65	44	19	6/6	LP[2]	Not taken		Not taken		
Reared	11.0	Postfl.	72	49	19	6/6	11/?	2+9		Not taken		
Reared	12.2	Juv.	72	47	19	6/6	11/11	3+7		Not taken		
Reared	15.9	Juv.	74	49	20	6/6	12/12	3+8		Not taken		
Reared	16.9	Juv.	72	48	19	6/6	10/11	3+7		Not taken		
Santo Tomas Bay, B.C.	19.5 26.5	Juv.	67 70	47 49	19 19	6/6 6/6	10/10 11/11	2+7 3+7		Not taken Not taken		

[1]Prefl. - preflexion; E fl. - early flexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

differentiate progressively anteriorward. A number of specimens, 5.3-5.8 mm NL with the notochord still straight, possess 2+2 or 3+3 caudal rays. The complete complement of 10+9 caudal rays is present on specimens 7.0 mm NL and larger. Flexion occurs in larvae between 6.1 and 7.0 mm NL (Figure 11B). By the time the caudal ray complement is fully formed, the rays are aligned in a terminal position (Figure 11C). The hypurals are observed as cartilaginous plates before they ossify. There are two superior and two inferior hypurals[3] in pleuronectid flatfishes. The

[3]We include the "parhypural" as a hypural bone. In flatfishes it is a splinter bone without remnant of a haemal arch.

TABLE 11.—Development of vertebral column, caudal fin rays, and caudal fin supporting bones in larvae of *Pleuronichthys verticalis*.

Station	Body length	Stage[1]	Precaudal vertebrae[2]		Caudal vertebrae[2]				Total vert.[3]	C fin rays	Ural bones[2]				
											Sup. hyp.		Inf. hyp.		
			n.pr.	centra	n.pr.	h.pr.	centra	Ural centrum			Upper	Mid	Mid	Lower	Epural
6609-97.29	5.3 NL	Prefl.	0	0	0	0	0	0	0	2+2	0	0	0	0	0
7503-90.27.6	5.6	Prefl.	0	0	0	7	0	0	7*	2+2	0	0	0	0	0
—	5.5	Prefl.	4+2	0	14	14	0	0	20*	3+3	0	0	0	0	0
6507-107.30	5.8	Prefl.	6+3	0	15	15	0	0	24*	3+3	0	0	0	0	0
5708-117.26	5.7	Prefl.	7+5	0	16	16	0	0	28*	3+3	0	0	0	0	0
6507-107.30	5.8	Prefl.	7+4	0	17	17	0	0	28*	3+3	0	0	0	0	0
5708-117.26	6.1	E fl.	13	0	19	20	0	0	33*	4+4	0	0	0	0	0
—	7.0	L fl.	13	0	22	22	0	0	35*	8+8	0	0	0	0	0
6606-97.29	6.9	L fl.	13	13	22	22	20	1	36	9+9	0	X	X	X	0
—	7.0 SL	Postfl.	13	13	23	23	23	1	37	10+9	0	X	X	X	X
6407-83.43	7.1	Postfl.	13	13	22	22	22	1	36	10+9	0	X	X	X	X
5110-100.40	7.3	Postfl.	13	13	22	22	22	1	36	10+9	X	X	X	X	X
6606-97.29	8.3	Postfl.	13	13	22	22	22	1	36	10+9	X	X	X	X	X
Reared	11.0	Postfl.	13	13	24	23	23	1	37	10+9	X	X	X	X	X
Reared	12.2	Juv.	13	13	22	22	22	1	36	10+9	X	X	X	X	X
Reared	15.9	Juv.	13	13	22	22	22	1	36	10+10	X	X	X	X	X
Reared	16.9	Juv.	13	13	22	22	22	1	36	10+9	X	X	X	X	X
Santo Tomas Bay, B.C.	19.5	Juv.	13	13	23	23	23	1	37	10+9	X	X	X	X	X
	26.5	Juv.	13	13	23	23	23	1	37	10+9	X	X	X	X	X

[1]Prefl. - preflexion; E fl. - early flexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.
[2]Abbreviations in heading: n.pr. - neural process; h.pr. - haemal process; vert. - vertebrae; Sup. hyp. - Superior hypurals; Inf. hyp. - Inferior hypurals.
[3]Asterisk indicates incomplete count.

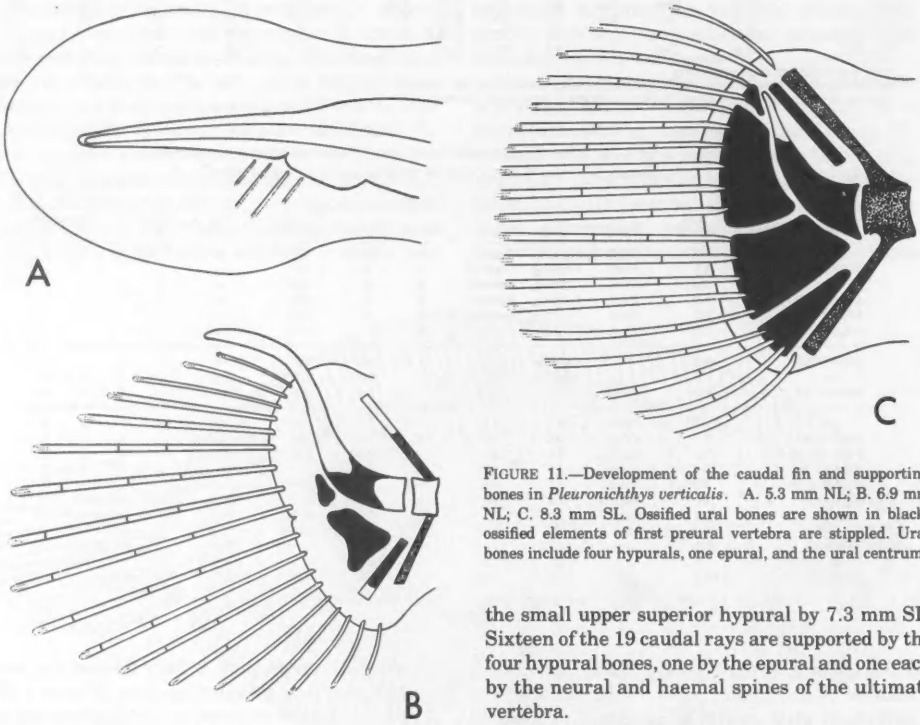


FIGURE 11.—Development of the caudal fin and supporting bones in *Pleuronichthys verticalis*. A. 5.3 mm NL; B. 6.9 mm NL; C. 8.3 mm SL. Ossified ural bones are shown in black; ossified elements of first preural vertebra are stippled. Ural bones include four hypurals, one epural, and the ural centrum.

main superior hypural and the two inferior hypurals are ossifying in specimens 6.9 mm NL and larger, the single epural by 7.0 mm SL, and the small upper superior hypural by 7.3 mm SL. Sixteen of the 19 caudal rays are supported by the four hypural bones, one by the epural and one each by the neural and haemal spines of the ultimate vertebra.

The vertebral column begins to ossify at about the same time rays begin forming in the caudal fin (Table 11). A 5.6-mm NL specimen which has 2+2 caudal rays has the first seven haemal processes of

the caudal group of vertebrae forming. A slightly more advanced 5.5-mm NL specimen has 14 opposing neural and haemal processes of caudal vertebrae formed as well as the four anteriormost and last two precaudal neural processes. A neural or haemal process consists of two portions—a divided basal portion that forms the neural or haemal arch ending in the second portion as a terminal spine. On the 5.5-mm NL specimen, only the tips of the neural spines of the caudal group are ossified. Of the precaudal group, ossification first occurs in the arched portion of the anterior four neural processes and on the tips only of the last two precaudal neural spines. On a 5.8-mm NL specimen with the first 7 and last 4 precaudal neural processes and 17 pairs of neural and haemal processes in the caudal group ossifying, all of the neural processes except those of the 7 anterior precaudal vertebrae were ossifying initially from both ends, i.e., from the distal tips of the neural spines and from the basal portion of the neural arches, with ossification from both ends proceeding medially (Figure 12A). In a 6.1-mm NL specimen all 13 precaudal neural processes and 19 neural and haemal processes in the caudal group are ossified (Figure 12B). A 7.0-mm NL late flexion specimen has all neural and haemal processes ossified except those on the terminal preural vertebra, but no centra are ossified. A 6.9-mm NL specimen, with all neural and haemal processes ossifying, has various stages of vertebral centra ossification with initial ossification of centra occurring below the bases of the neural and haemal arches and then filling in medially; only the two vertebral centra adjacent to the urostyle lack any ossification; the six vertebrae immediately forward of these have the best ossified centra. A 7.0-mm SL specimen has all centra ossified.

The bases of the dorsal and anal fins are present on larvae as small as 5.3 mm NL and rays begin to form by late flexion. Full complements of dorsal and anal fin rays are present on most postflexion specimens. Buds of the pelvic fins were first seen on a 6.1-mm NL specimen, and the complete count of six rays per fin is developed by 8.3 mm SL. Pectoral rays form only toward the end of the transformation stage after the left eye has nearly completed its migration to the right side.

Branchiostegal rays form progressively anteriorward during the period of caudal fin forma-

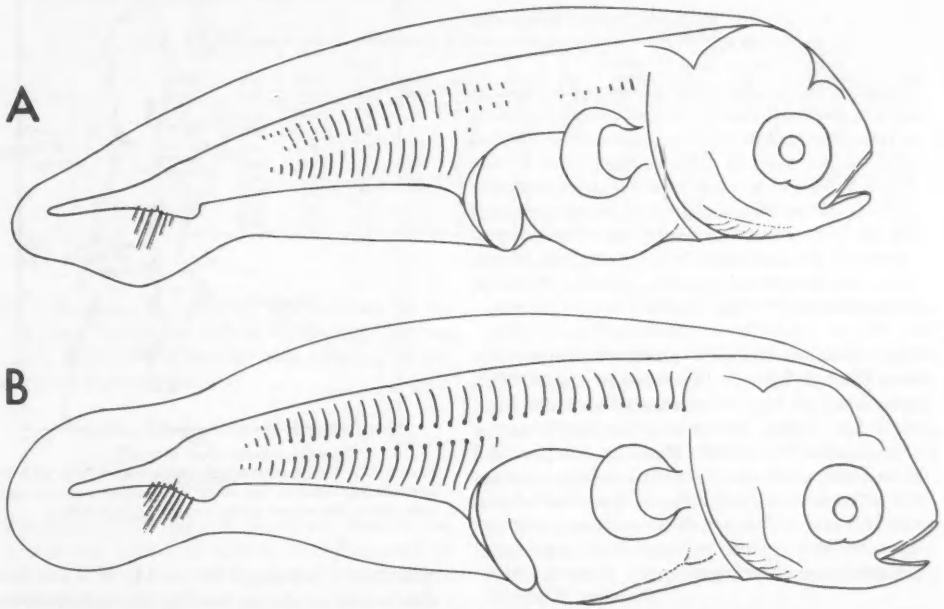


FIGURE 12.—Ossification pattern of the axial skeleton of *Pleuronichthys verticalis*: A. 5.8 mm; B. 6.1 mm.

tion between 5.6 and 6.9 mm NL, and the full count of seven rays per side is present on late flexion specimens. Gill rakers begin to develop by late flexion, but the full count is not obtained until the early juvenile stage. Few teeth form during the larval period. Only a single tooth is developed on the right side of the upper jaw in postflexion larvae, compared with 3-6 on the left side of this jaw. The disproportion is less marked in the lower jaw, with 3-5 teeth on the right side compared with 5-7 on the left side.

Distribution.—This species ranges from Point Reyes, Calif., south to Magdalena Bay, Baja California, with an isolated population at the northern end of the Gulf of California (Norman 1934; Fitch 1963). Eggs and larvae are common in our collections, particularly at inshore stations located over the continental shelf, with only an occasional specimen being taken more than 60 mi from the coast (Figure 13).

Pleuronichthys ocellatus Starks and Thompson (Gulf turbot) Figure 14

Literature.—Neither eggs nor larvae have been described previously.

Distinguishing characters.—This species may only be confused with *P. verticalis* or *H. guttulata* which cooccur with it in the upper Gulf of California. Larvae may be distinguished from *P. verticalis* by the lower total vertebral number of 34 or 35 and pigmentation differences. The larger size of larvae, lack of pterotic spines, and different pigment pattern separate it from *H. guttulata*. Meristics of the larvae and juveniles, given in Table 12, are distinctive for the species.

Pigmentation.—Only two postflexion larvae (6.6 mm SL and 7.0 mm SL) were available. Both specimens are heavily pigmented and somewhat resemble similar stages of *P. verticalis* larvae (Figure 14 vs. Figure 9D). However, smaller sized larvae of *P. ocellatus* are heavier in pigment than *P. verticalis* in regions of the head and dorsal and anal fin pterygiophores. Only the margin of the opercle, otic region, pectoral fin, and caudal peduncle remain unpigmented.

Morphology.—Larvae of *P. ocellatus* are intermediate in size between comparable stages of *P. ritteri* and *P. verticalis* (Table 13). It is the most slender-bodied species having the smallest body depth ratios in the postflexion larval stage within its genus (Table 5).

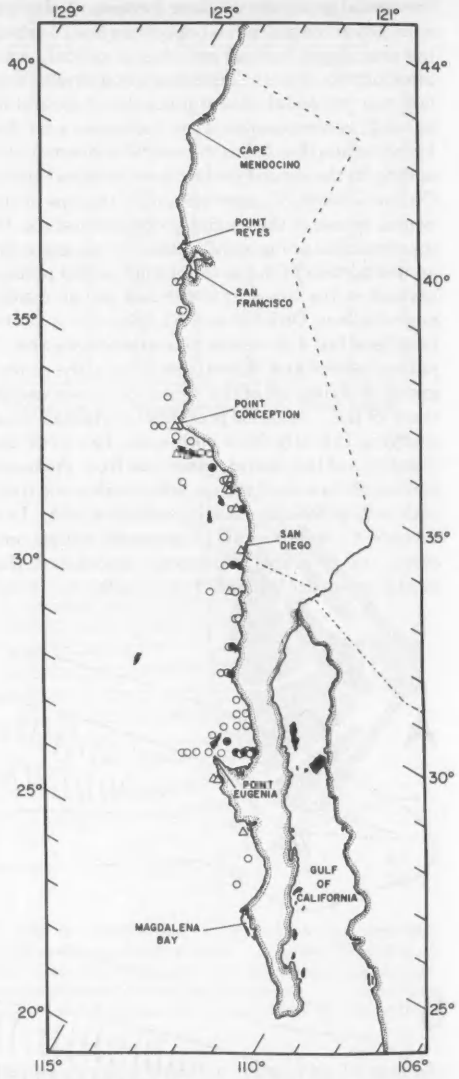


FIGURE 13.—Distribution of eggs and larvae of *Pleuronichthys verticalis* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

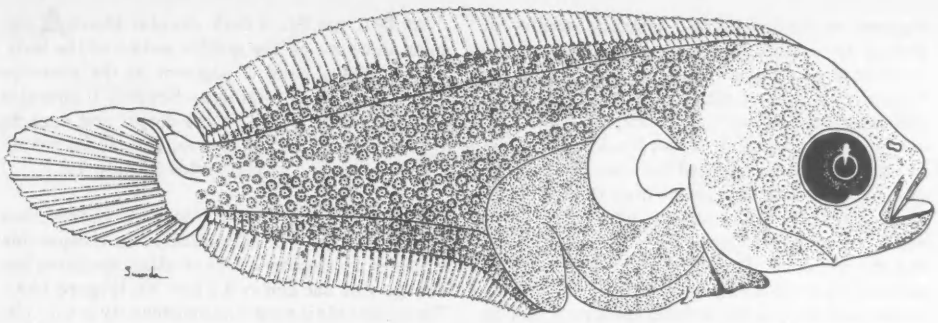


FIGURE 14.—*Pleuronichthys ocellatus* larva, 7.0 mm.

TABLE 12.—Meristics of larvae and juveniles of *Pleuronichthys ocellatus*.

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5604-111.G.14	6.6 SL	Postfl.	65	49	19	ca. 4/4	LP[2]				
5604-109.G.25	7.0	Postfl.	73	50	19	ca. 3/3	LP[2]				
Upper Gulf of California	19.2	Juv.	64	45	19	6/6	10/11	12	22	34	X-ray
	22.0	Juv.	73	49	19	6/6	10/10	12	24	36	X-ray
	24.0	Juv.	67	48	19	6/6	—/11	12	22	34	X-ray
	24.5	Juv.	71	51	19	6/6	11/10	12	23	35	X-ray
	25.0	Juv.	70	50	19	6/6	11/10	12	22	34	X-ray
	25.5	Juv.	68	46	19	6/6	10/10	12	23	35	X-ray

[1]Postfl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

TABLE 13.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys ocellatus*.

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base	Body depth at anus	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5604-111.G.14	6.6 SL	Sym.	Flexed	3.2	2.0	0.30	0.54	0.56	2.2	2.2	0.50	0.40	1.9
5604-109.G.25	7.0	Sym.	Flexed	3.3	2.1	0.40	0.62	0.56	2.3	2.3	0.52	0.50	2.1
Upper Gulf of California	19.2	Over	Juv.	7.0	5.7	0.83	1.8	—	8.2	9.0	2.4	1.2	5.0
	22.0	Over	Juv.	7.0	6.2	0.91	1.9	—	9.4	9.8	2.8	1.4	5.2
	24.0	Over	Juv.	7.7	6.5	0.91	2.1	—	9.4	10.2	2.8	1.4	5.7
	24.5	Over	Juv.	7.4	6.8	1.1	2.3	—	10.5	11.0	3.2	1.5	5.5
	25.0	Over	Juv.	7.5	6.7	0.83	2.5	—	10.4	11.2	3.2	1.7	5.7
	25.5	Over	Juv.	8.5	6.8	0.91	2.3	—	10.7	11.7	3.1	1.8	6.0

[1]Sym. - symmetrical.
[2]Juv. - juvenile.

Distribution.—This species is restricted to the northern half of the Gulf of California (Norman 1934; Fitch 1963). Larvae were collected at two stations in the upper Gulf.

Pleuronichthys ritteri Starks and Morris (spotted turbot) Figures 15-17

Literature.—The egg of *P. ritteri* was described by Orton and Limbaugh (1953) and illustrated by White (1977). Larvae of this species have not been described previously.

Distinguishing characters.—Larval stages of this species may be confused with *P. verticalis* and *H. guttulata*. Characters of preflexion and flexion larvae which separate it from *P. verticalis* include the lack of triangular clusters of pigment on the finfold, less pigment on the tail with 8 or 9 unpigmented myomeres compared with 3-5 in *P. verticalis*, and a more robust body. Postflexion larvae are more heavily pigmented, particularly on the dorsal and anal fin pterygiophores, and are smaller than comparable stages of *P. verticalis*. Distinguishing characters for newly transformed and early juvenile stages have been discussed earlier under *P. verticalis*.

Characters for distinguishing yolk-sac larvae of *P. ritteri* from *H. guttulata* include the presence of

pigment on the finfolds of *P. ritteri*, a smaller oil globule (average 0.10 vs. 0.14 mm), lack of pigment on the oil globule, and presence of pigment ventrally near the tip of the notochord. Distinctive characters of preflexion and flexion larvae of *P. ritteri* include the lack of pterotic spines on the head which is more rounded than on preflexion *H. guttulata*, the lack of pigment from the top of the head posteriorly to the nape, a more robust head and trunk (compare Figure 15D with Figure 19D), and the presence of small pigment spots on the pectoral fin blade along its margin or base. Postflexion and early transforming specimens can be distinguished by a deeper and shorter caudal peduncle, a more robust body, and the origin of the dorsal fin on the future blind side of the head instead of on the medial line of the head as found in *H. guttulata*.

Pigmentation.—Yolk-sac larvae are heavily pigmented with the exception of the last 8 or 9 myomeres. Pigment is also scattered on the remnant of the yolk sac, on the dorsal and ventral finfolds, and ventrally on the tail near the tip of the notochord (Figure 15A). Except for the appearance of pigment along the margins of the pectoral fin blade, no significant changes in pigmentation occur in early preflexion larvae of ca. 3.0 mm NL (Figure 15B).

By 4.0 mm NL, pigment found earlier along the top of the head posterior to the nape is lost, leaving an unpigmented streak which persists until flexion of the notochord is complete at 5.5 mm NL (Figures 15C, D; 16A, B). Ventral pigment is similarly lost on the abdominal region, resulting in an unpigmented lower abdomen in late preflexion and flexion specimens. Marginal pectoral fin pigment present on larvae to about 3.3 mm NL, changes to small, discrete spots on the fin membrane along its base. These melanophores persist through postflexion larvae until the pectoral fin differentiates into a small, rayed fin by ca. 10.0 mm SL (Figures 16C, 17).

Pigment on the tail extends posteriad the same distance in flexion larvae as in preflexion larvae, but in postflexion larvae the tail pigment fills in posteriorly to the terminal dorsal and anal fin rays. In later postflexion and transformation stages, the head, trunk, and tail, except the caudal peduncle, are completely covered with pigment which extends over the dorsal and anal fin pterygiophores (Figures 16C, 17).

At 10.0 mm SL, a dark circular blotch of pigment develops on the middle section of the body, with a heavy band of pigment at the posterior extreme of body pigment. Several triangular patches are clustered on the dorsal and anal fin rays above the pterygiophores. The caudal peduncle area remains unpigmented (Figure 17).

Morphology.—Larvae of *P. ritteri* are the smallest among species of *Pleuronichthys* in comparable stages of development. Our smallest specimen has a large yolk sac and is 2.1 mm NL (Figure 15A). The oil globule is positioned posteriorly in the yolk mass and measures 0.11 mm in diameter. The left eye begins to migrate at about 6.0 mm SL and migration of the eye is completed before 10.0 mm SL (Table 14). The smallest available juvenile was 12.7 mm SL.

The gut develops as in other *Pleuronichthys* but coiling begins earlier, at about 3.0 mm NL, and the terminal section of the gut is in a vertical position in most specimens >4.0 mm NL.

The head is relatively larger in preflexion larvae of *P. ritteri* than in the other species (Table 5). Relative head length increases throughout the larval period, then is moderately reduced at transformation. Mean relative snout length increases in *P. ritteri* larvae undergoing notochord flexion and decreases during subsequent stages, but in other species of *Pleuronichthys* it decreases during all major phases of larval development. Relative eye size is largest in preflexion larvae, becomes reduced in later larval stages, and increases at transformation.

The early larvae of *P. ritteri* are the deepest bodied species of *Pleuronichthys*. Mean relative body depth measured at the base of the pectoral fin is greater during preflexion and flexion stages of the notochord than in any other species. In postflexion larvae, however, mean relative body depth is markedly less than in *P. decurrens* and about equal to that in *P. coenosus* and *P. verticalis* (Table 5).

Fin and axial skeleton formation.—Early caudal formation involving thickening in the hypural area of the developing caudal fin occurs on larvae 4.3-5.1 mm NL (Table 15). Caudal rays are forming on larvae as small as 4.5 mm NL, with a simultaneous initiation of flexion of the notochord. Specimens between 4.5 and 5.6 mm NL undergo notochord flexion. Our smallest specimen with a fully flexed notochord is 5.3 mm SL. The full

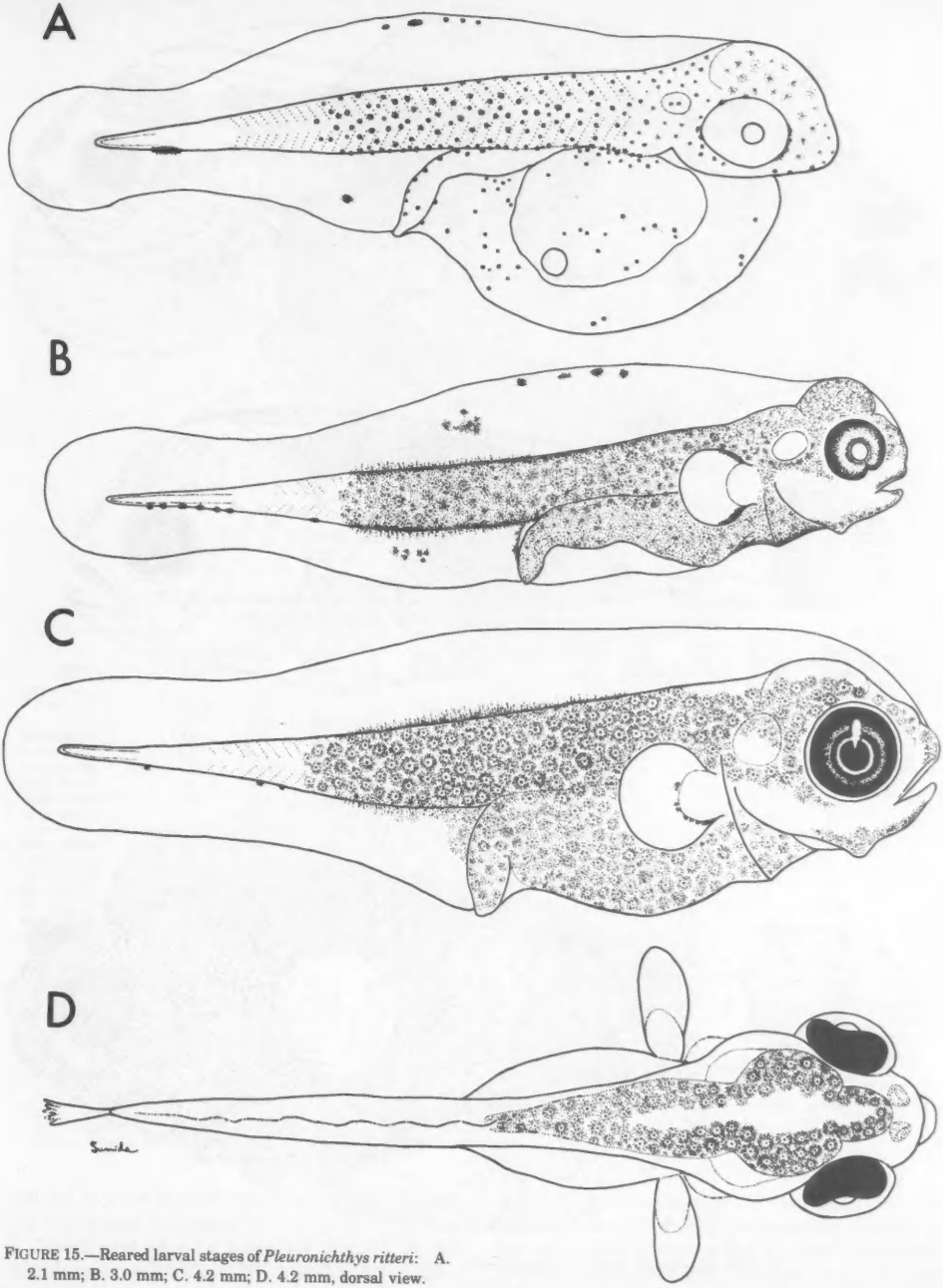


FIGURE 15.—Reared larval stages of *Pleuronichthys ritteri*: A. 2.1 mm; B. 3.0 mm; C. 4.2 mm; D. 4.2 mm, dorsal view.

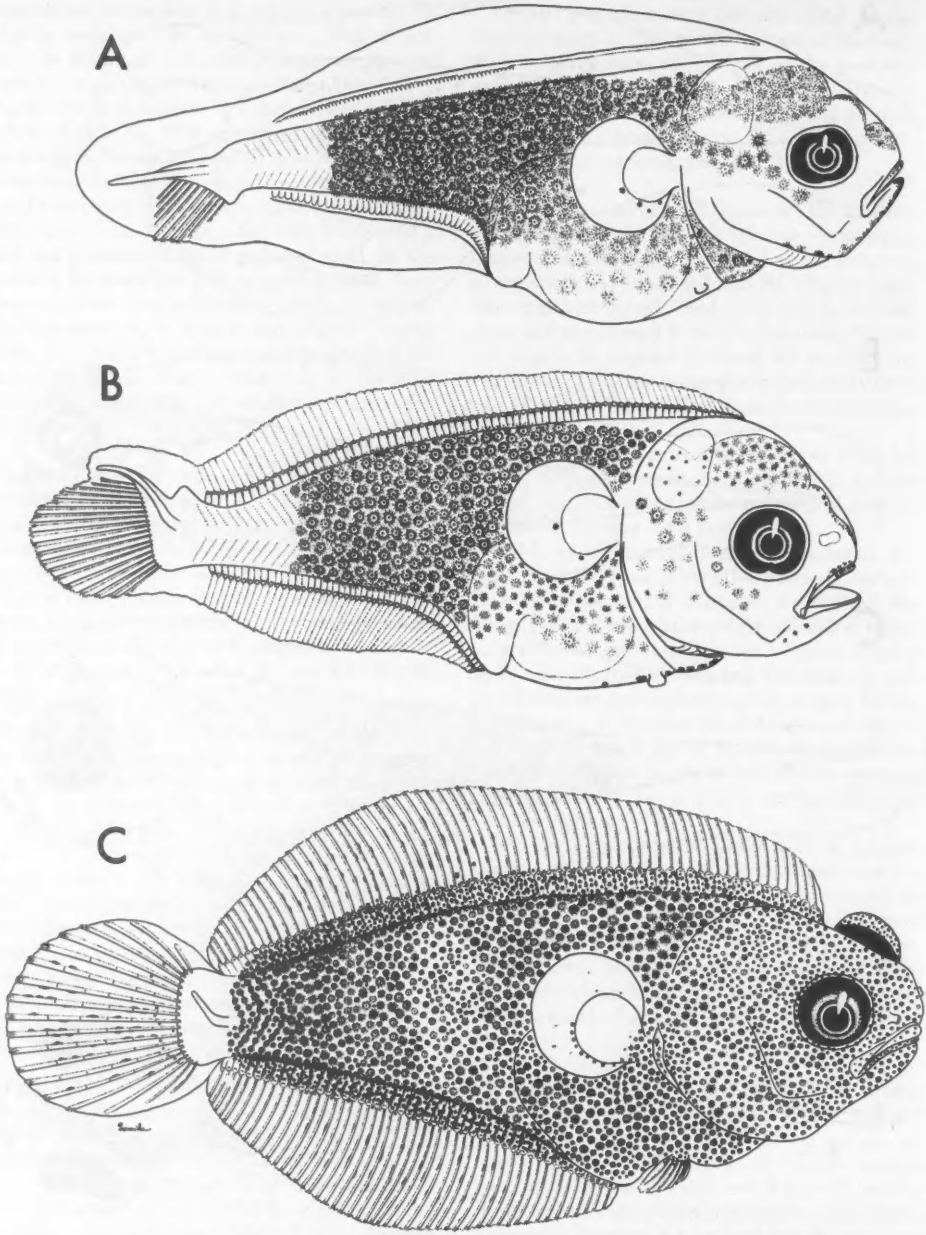


FIGURE 16.—Larval stages of *Pleuronichthys ritteri*: A. 5.6 mm; B. 5.5 mm; C. 6.4 mm.

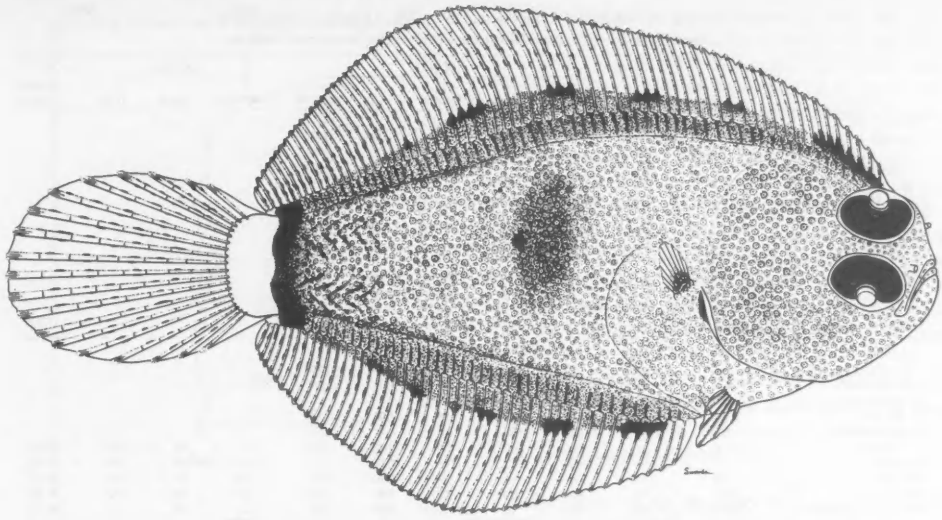


FIGURE 17.—Transforming specimen of *Pleuronichthys ritteri*, 10.0 mm.

TABLE 14.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys ritteri*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle to length	Snout to origin pelvic fin
Off La Jolla, Calif.	2.1 NL	Sym.	Str.	1.2	0.50	0.10	0.24	0.20	0.20	0.38	—	—	—
	3.0	Sym.	Str.	1.4	0.60	0.12	0.26	0.22	0.42	0.42	—	—	—
7412-123.36	3.3	Sym.	Str.	1.6	0.80	0.14	0.28	0.24	0.78	0.58	—	—	—
Off La Jolla	4.2	Sym.	Str.	2.2	1.0	0.18	0.40	0.32	0.96	0.86	—	—	—
5709-117.26	4.3	Sym.	Str.	2.1	1.1	0.20	0.40	0.36	1.2	1.2*	—	—	—
7207-123.36	4.4	Sym.	Str.	2.1	1.1	0.24	0.34	0.32	1.0	0.9	—	—	—
6204-120.25	5.0	Sym.	Str.	2.2	1.2	0.20	0.38	0.38	1.2	1.1*	—	—	—
5708-120.25	5.1	Sym.	Str.	2.5	1.4	0.24	0.46	0.40	1.8*	1.7*	—	—	1.3
6507-120.35	4.5	Sym.	E fl.	2.3	1.4	0.32	0.44	0.42	1.6*	1.6*	—	—	1.2
5506-120.40	4.8	Sym.	E fl.	2.3	1.4	0.28	0.40	0.38	1.5*	1.7*	—	—	1.4
5510-117.26	5.5	Sym.	Midfl.	2.7	1.2	0.34	0.52	0.48	2.0*	1.9*	—	—	1.6
7501-120.25	5.6	Sym.	Midfl.	2.7	1.5	0.26	0.46	0.40	1.8*	1.5*	—	—	1.4
5112-120.35	5.3 SL	Sym.	Flexed	2.7	1.7	0.30	0.52	0.52	2.2*	2.2*	0.50	0.36	1.4
5802-137.23	6.0	Migr.	Flexed	2.9	2.0	0.32	0.60	0.54	2.4*	2.7*	0.66	0.30	1.8
Off La Jolla	6.4	Migr.	Flexed	2.6	2.2	0.40	0.64	0.60	2.5*	2.7*	0.76	0.38	2.0
Sebastian Viscaino Bay, B.C.	7.5	A. over	Flexed	3.0	2.6	0.40	0.80	0.64	2.9*	3.0*	1.0	0.48	2.7
7501-120.22.4	8.5	A. over	Flexed	2.8	2.7	0.40	0.86	?	3.6*	3.6*	1.1	0.44	2.3
Off La Jolla	10.0	Over	Flexed	3.1	3.1	0.48	1.0	0.80	4.2*	4.2*	1.4	0.60	2.6
Reared	12.7	Over	Juv.	4.2	3.8	0.36	1.4	1.0	5.1*	5.4*	1.4	0.76	3.4
Reared	15.0	Over	Juv.	4.5	4.2	0.48	1.6	1.2	5.9*	6.1*	1.8	1.0	3.9
Reared	16.7	Over	Juv.	5.2	4.7	0.48	1.8	1.4	6.2*	6.4*	2.0	1.1	4.2
Off San Juanico, B.C.	23.0	Over	Juv.	7.2	6.8	0.83	2.2	?	9.7*	9.7*	2.6	1.2	5.8

[1]Sym. - symmetrical; Migr. - migrating; A. over - About over.
[2]Str. - straight; E fl. - early flexion; Midfl. - midflexion; Juv. - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

caudal count of 19 rays was observed on a 6.0-mm SL postflexion specimen.

Dorsal and anal fin bases are forming in the finfold on larvae 4.3 mm NL, and the full complement of rays develops by 6.0 mm SL. Pelvic fin buds are evident during early caudal formation but rays are first observed on a 6.0-mm specimen. Pectoral rays were fully formed on a 10.0-mm

TABLE 15.—Meristics of larvae and juveniles of *Pleuronichthys ritteri*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
Off La Jolla, Calif.	2.1 NL	Yolk-sac	0	0	0	0	LP[2]				
	3.0	Prefl.	0	0	0	0	LP[2]				
7412-123.36	3.3	Prefl.	0	0	0	0	LP[2]				
Off La Jolla	4.2	Prefl.	0	0	0	0	LP[2]				
5709-117.26	4.3	Prefl.	Forming	Forming	Forming	0	LP[2]				
7207-23.36	4.4	Prefl.	Forming	Forming	Forming	0	LP[2]				
6204-120.25	5.0	Prefl.	Forming	Forming	Forming	0	LP[2]				
5708-120.25	5.1	Prefl.	Forming	Forming	Forming	Bud	LP[2]				
6507-120.35	4.5	E fl.	Forming	Forming	ca. 6	Bud	LP[2]				
5506-120.40	4.8	E fl.	Forming	Forming	ca. 4	Bud	LP[2]				
5510-117.26	5.5	Midfl.	Forming	Forming	ca. 8	Bud	LP[2]				
7501-120.25	5.6	Midfl.	Forming	Forming	ca. 8	Bud	LP[2]				
5112-120.35	5.3 SL	Postfl.	ca. 60	ca. 45	16	Bud	LP[2]				
5802-137.23	6.0	Postfl.	72	49	19	6/6	LP[2]				
Off La Jolla	6.4	Postfl.	65	45	19	6/6	LP[2]				
Sebastian Viscaino Bay, B.C.	7.5	Postfl.	70	48	19	6/6	LP[2]				
7501-120.22.4	8.5	Postfl.	69	51	19	6/6	LP[2]				
Off La Jolla	10.0	Postfl.	68	47	19	6/6	9/9	12	23	35	X-ray
Reared	12.7	Juv.	69	47	19	6/6	10/11	12	23	35	X-ray
Reared	15.0	Juv.	64	44	19	6/6	10/11	12	23	35	X-ray
Reared	16.7	Juv.	65	44	19	6/6	11/11	12	22	34	X-ray
Off San Juanico, B.C.	23.0	Juv.	68	49	Damaged	6/6	9/9	12	23	35	X-ray

[1]Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; Postfl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

larva. A radiograph of this specimen showed 12 precaudal and 23 caudal vertebrae, the typical count for this species.

Distribution.—This species ranges from Morro Bay, Calif., to Magdalena Bay, Baja California (Fitch 1963; Miller and Lea 1972; Fierstine et al. 1973). Our egg and larval material, which was collected between southern California and Magdalena Bay, Baja California, shows a markedly coastal, inshore distribution for *P. ritteri*, with a majority of collections made over or near the continental shelf (Figure 18).

Hypsopsetta guttulata Girard (diamond turbot) Figures 19-22

Literature.—Orton and Limbaugh (1953) and Orton (1953) briefly described the eggs of *H. guttulata*. Eldridge (1975) described and illustrated larvae of this species, and noted the average size of its egg and oil globule. Although the larval series is quite well described in Eldridge (1975) (except for the omission of the pterotic spine on the head), we are including information about distinguishing characters, pigmentation, etc. to facilitate identification.

Distinguishing characters.—Larvae of *H. guttulata* are distinguishable from species of *Pleuronichthys*, except for *P. ritteri*, by their lower total vertebral number, by attaining comparable stages of development at smaller sizes, and by the presence of a pterotic spine on each side of the head in yolk-sac larvae to midflexion larvae. In the genus *Pleuronichthys*, only *P. decurrens* develops pterotic spines. (See Distinguishing characters for *P. decurrens*.)

The only species with which larval *H. guttulata* may be confused is *P. ritteri* because of its relatively small size and somewhat similar pigment pattern. (See Distinguishing characters for separating larvae of the two species discussed under *P. ritteri*.)

Pigmentation.—Yolk-sac larvae are heavily pigmented on the head, trunk, and for a short distance on the tail, with the posteriormost 9 or 10 myomeres remaining unpigmented (Figure 19A). Pigment spots are scattered over the ventral and posterior surfaces of the yolk sac and oil globule, and over the terminus of the gut.

Preflexion larvae show little change in pigment pattern. One or two melanophores develop on the pectoral fin base. The isthmus has a line of pigment spots, and the entire abdominal area is covered with pigment (Figure 19B).

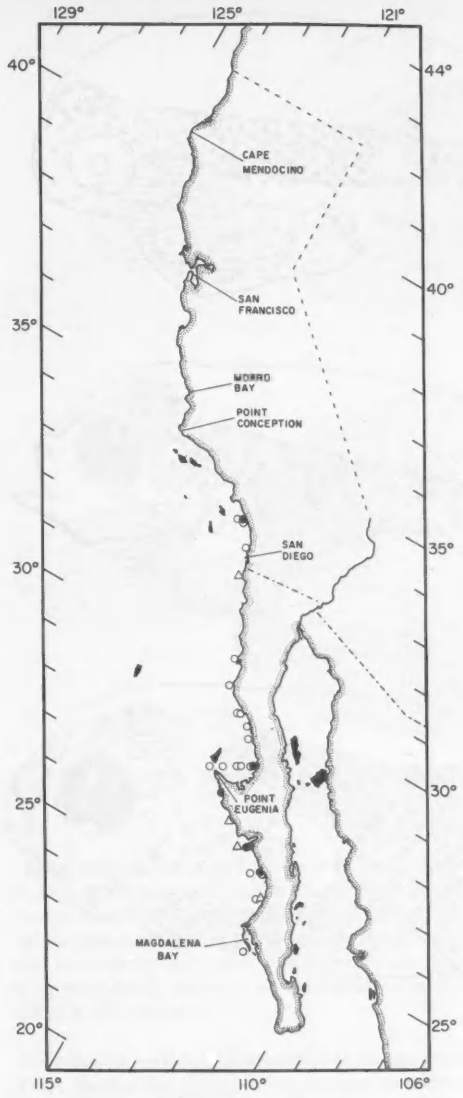


FIGURE 18.—Distribution of eggs and larvae of *Pleuronichthys ritteri* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

At the initiation of dorsal and anal fin formation, the tail pigment spreads out dorsally and ventrally onto the finfold, resulting in conspicuous dark mounds of pigment opposing each other in the area between the body and the dorsal and anal fin bases (Figure 19C). The tops of the head, nape, and shoulder area are pigmented in contrast to *P. ritteri*, which has an unpigmented streak dorsally (Figure 19D). Flexion, postflexion, and early transforming specimens maintain the earlier pigment pattern and the only obvious change is a slight posteriad extension of trunk pigment, leaving 5 or 6 unpigmented myomeres posteriorly compared with 9 or 10 in earlier stages (Figure 20). The base of the pectoral fin acquires more pigment spots in postflexion larvae, and pigment on the head similarly increases in density (Figure 20B).

Preserved small juveniles are brownish-black with numerous small, dark spots scattered over the body and pterygiophores, giving them a mottled appearance (Figure 21).

Morphology.—Our smallest yolk-sac larva is 2.2 mm NL and has a posteriorly positioned oil globule 0.14 mm in diameter (Figure 19A). The left eye is beginning to migrate in a specimen 4.4 mm SL and is complete in a 7.3-mm SL larva (Table 16). The smallest available juvenile was 11.2 mm SL.

A major distinguishing feature of *Hypsopsetta* larvae is the presence of a pterotic spine on each side of the head. The spines are present on the smallest yolk-sac larva and are prominent in most preflexion larvae. The spines begin to regress on late preflexion larvae, and are totally regressed in late flexion specimens. In *P. decurrens* the spines are well developed throughout the larval period and begin to regress late in the postflexion stage.

Although mean relative body depth of *H. guttulata* larvae increases with development, it is slightly less in postflexion specimens than in any species of *Pleuronichthys*, except *P. ocellatus* (Table 5). In newly transformed juveniles, however, relative body depth is greater than in any species of *Pleuronichthys*. As a juvenile, *H. guttulata* assumes a diamond-shaped body form.

Relative body width is useful to separate *Hypsopsetta* larvae from those of *P. ritteri*. As shown in Figures 15D and 19D, larvae of *Hypsopsetta* have narrower bodies.

Fin formation.—The caudal fin forms on larvae between 4.0 and 5.2 mm NL and is complete on some specimens as small as 4.4 mm (Table 17). The dorsal and anal fins form simultaneously with the

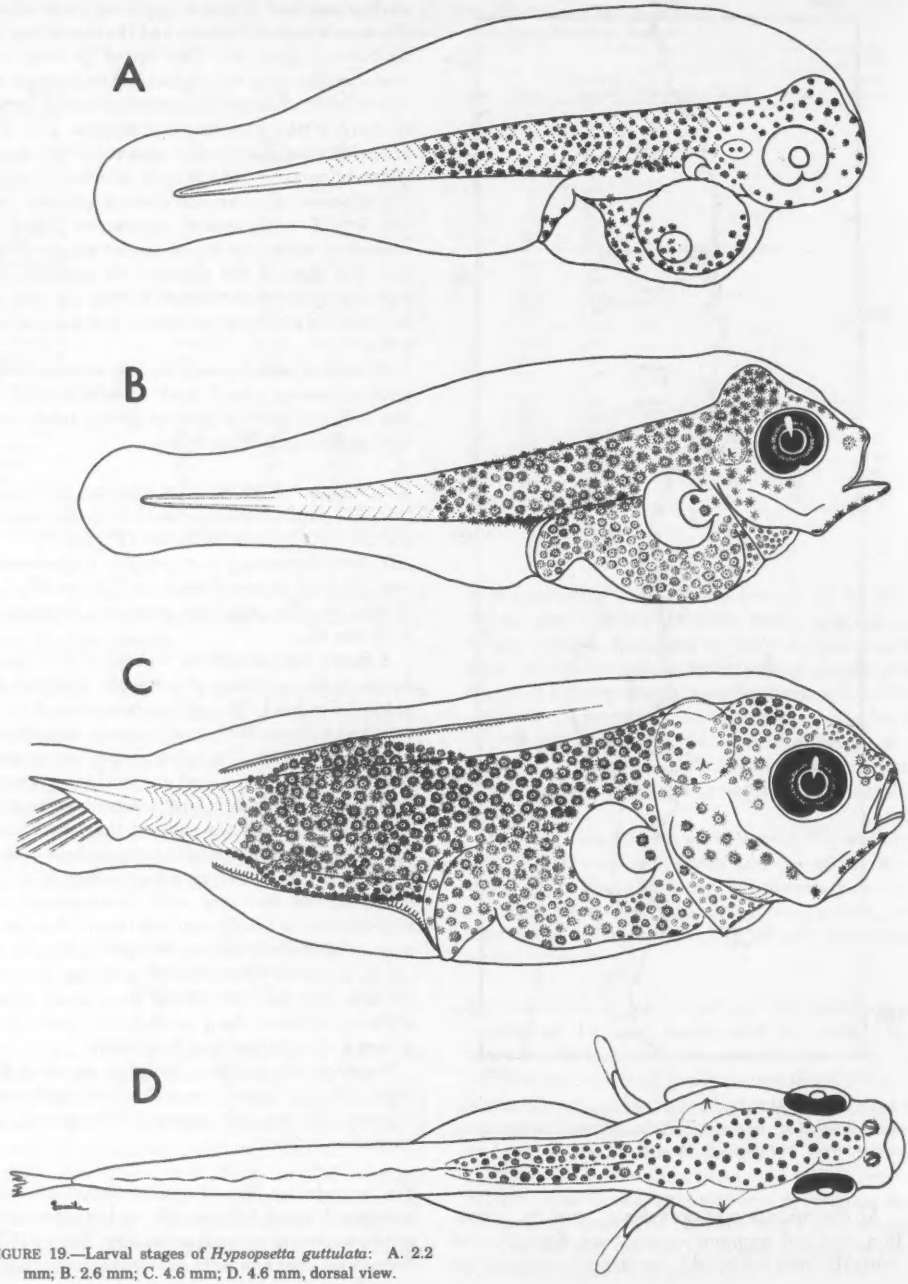


FIGURE 19.—Larval stages of *Hypsopsetta guttulata*: A. 2.2 mm; B. 2.6 mm; C. 4.6 mm; D. 4.6 mm, dorsal view.

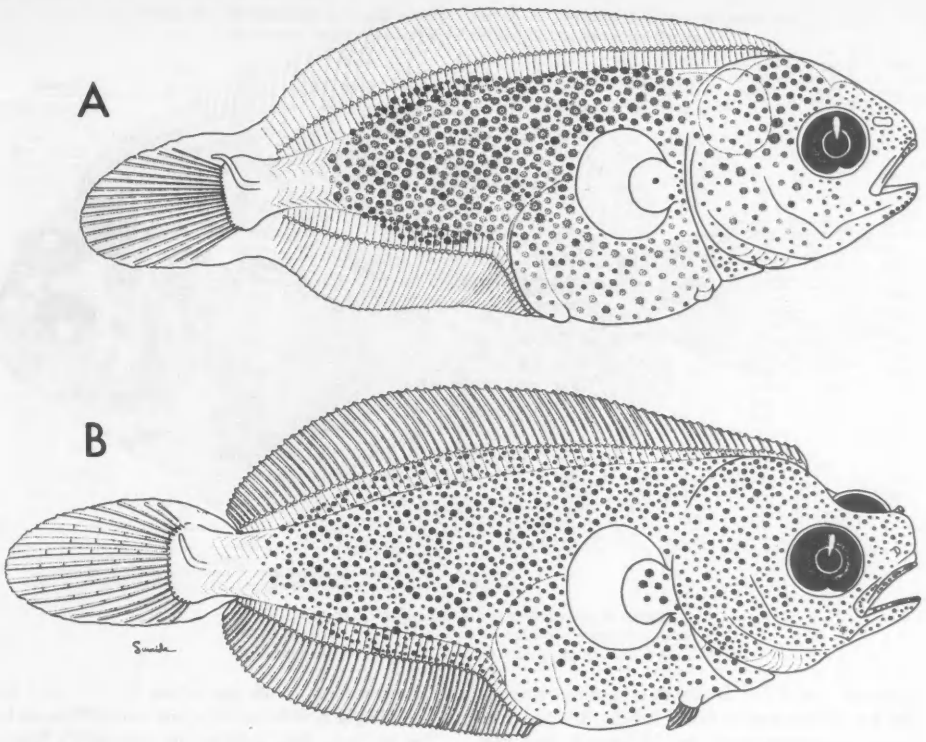


FIGURE 20.—Larval stages of *Hypsopsetta guttulata*: A. 5.9 mm; B. 6.6 mm.

caudal and are complete, or nearly so, on all postflexion specimens (4.4-8.8 mm SL). Pelvic fins are late in forming compared with their developmental pattern in *Pleuronichthys* larvae. Pelvic buds can be observed only after notochord flexion has been completed, and rays are first evident on the 6.6-mm SL specimen.

Distribution.—*Hypsopsetta guttulata* ranges from Cape Mendocino, Calif., to Magdalena Bay, Baja California, with an isolated population in the upper Gulf of California (Norman 1934; Fitch 1963). Egg and larval material examined by us was collected in bays along the coast, or at CalCOFI stations located over the continental shelf, a pattern of distribution similar to the habitat of *P. ritteri* (Figure 22).

Hippoglossina stomata Eigenmann and Eigenmann (bigmouth sole) Figure 23

Literature.—There is no published account of eggs and larvae of this species. However, Leonard (1971) described a larval series of *H. oblonga* from the western North Atlantic. Earlier, Agassiz and Whitman (1885) and Miller and Marak (1962) described the eggs and early-stage larvae of *H. oblonga*. Miller and Marak reported the egg size range as 0.91-1.12 mm (average 1.04 mm) with an oil globule diameter of ca. 0.17 mm. The larval size at hatching was 2.7-3.2 mm.

Distinguishing characters.—Preflexion larvae of *H. stomata* may be confused with early larvae of *P.*

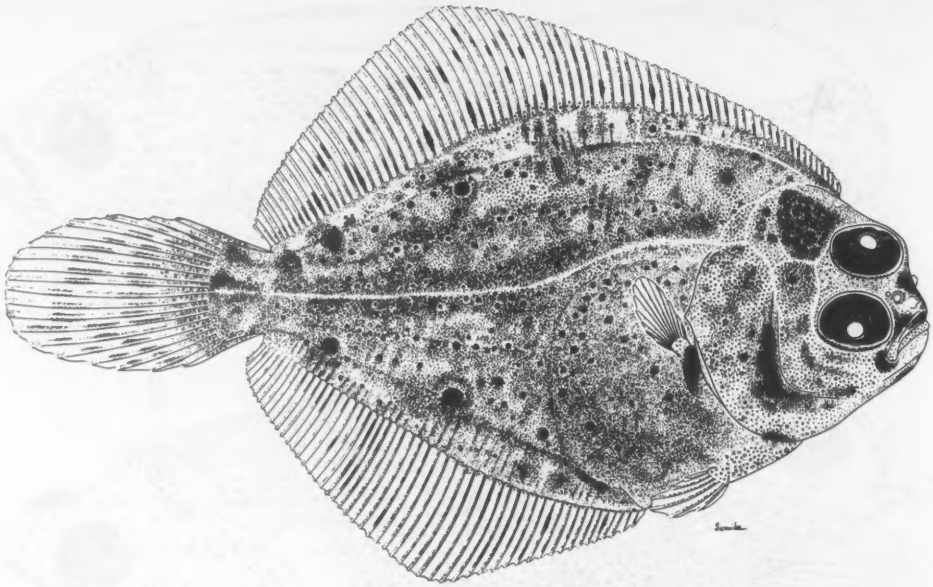


FIGURE 21.—Early juvenile of *Hypsopsetta guttulata*, 13.2 mm.

coenosus and *P. verticalis* due to similarities in size and pigmentation of the larvae, and the presence of pigment on the finfold dorsally and ventrally, posterior to the anus. Characters of *H. stomata* larvae which distinguish them from preflexion *P. coenosus* larvae include the presence of a pigment bar through the eye, heavy pigment on both sides of the pectoral fin base and a sprinkling of pigment on the pectoral blade, a more slender, elongate body, and a significantly smaller patch of dorsal finfold pigment. The same characters help to distinguish *H. stomata* from *P. verticalis*, except for the finfold pigmentation. *Pleuronichthys verticalis* has small, triangular-shaped pigment patches whereas *H. stomata* has a small rounded pigment cluster on the dorsal finfold and a broad patch on the ventral finfold. Larvae of *P. verticalis* are also smaller than *H. stomata* at similar developmental stages.

Larvae in the flexion stage and larger are readily separable from *Pleuronichthys* by the preopercular spines and development of several elongated dorsal rays in the anteriormost part of the dorsal fin. These do not develop on larval *Pleuronichthys* or *Hypsopsetta*.

Pigmentation.—Yolk-sac larvae (ca. 3.7 mm) are heavily pigmented on the trunk and tail except for the posteriormost part of the tail which is pigmented with several small spots dorsally and ventrally (Figure 23A). The upper head and abdominal region have scattered pigment, with a more concentrated bar of pigment on each side of the eye. Both sides of the pectoral fin base are conspicuously pigmented. Finfold pigment consists of a small, rounded patch at the edge of the dorsal finfold, and a broad patch on the ventral finfold, both situated posterior to the anus near the midpoint between the anus and tip of the tail (Figure 23A).

Preflexion larvae, 4.1-7.0 mm NL, undergo little change in pigmentation except to augment pigment in areas of the pectoral fin, abdominal region, and top of the head (Figure 23B).

On larvae forming the dorsal and anal fins, the dorsal finfold pigment spreads to include the area between the fin rudiments and body margin, and the ventral finfold pigment spreads both anteriorly and posteriorly (Figure 23C). Pigment on the pectoral fin base intensifies and also extends out onto the fin blade.

TABLE 16.—Morphometrics, in millimeters, of larvae and juveniles of *Hypsopsetta guttulata*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
San Diego Bay	2.2 NL	Sym.	Str.	1.1	0.38	0.08	0.17	0.13	0.18	0.28	—	—	—
King Harbor, Calif.	2.3	Sym.	Str.	1.1	0.46	0.12	0.20	0.17	0.18	0.34	—	—	—
7501-120.25	2.8	Sym.	Str.	1.4	0.68	0.12	0.26	0.22	0.62	0.52	—	—	—
7501-120.29	3.3	Sym.	Str.	1.7	0.82	0.20	0.30	0.24	0.82	0.72	—	—	—
San Diego Bay	3.6	Sym.	Str.	1.8	0.84	0.16	0.32	0.28	0.78	0.66	—	—	—
San Diego Bay	4.0	Sym.	Str.	2.0	0.88	0.20	0.36	0.30	0.88	0.84	—	—	—
7412-127.32.6	4.4	Sym.	Str.	2.2	0.90	0.20	0.37	0.32	1.0	0.92	—	—	—
7412-127.32.6	4.6	Sym.	E fl.	2.3	1.2	0.24	0.38	0.32	1.1	1.0	—	—	—
7501-120.22.4	4.9	Sym.	E fl.	2.4	1.3	0.22	0.40	0.36	1.2	1.1	—	—	—
7501-120.29	5.1	Sym.	E fl.	2.5	1.2	0.22	0.40	0.36	1.1	1.1	—	—	—
King Harbor	5.2	Sym.	L fl.	2.4	1.4	0.28	0.44	0.42	1.2	1.2	—	—	—
L.A. Harbor, Calif.	4.4 SL	Migr.	Flexed	2.2	1.6	0.30	0.48	0.42	1.8*	1.9*	0.40	0.40	1.4
La Jolla, Calif.	4.8	Migr.	Flexed	2.2	1.5	0.30	0.48	0.40	1.6*	1.7*	0.40	0.36	1.4
San Diego Bay	5.4	Migr.	Flexed	2.3	1.8	0.34	0.52	0.40	1.8*	1.9*	0.42	0.42	1.6
7501-120.22.7	5.9	Sym.	Flexed	3.1	1.8	0.32	0.50	0.46	2.0*	2.2*	0.44	0.48	1.9
7501-120.24	6.6	Migr.	Flexed	3.2	2.1	0.40	0.62	0.52	2.3*	2.4*	0.50	0.60	2.0
Reared	7.3	Over	Flexed	2.9	2.5	0.40	0.90	0.70	3.3*	3.5*	0.76	0.64	2.1
Reared	7.9	Over	Flexed	2.9	2.7	0.44	0.92	0.68	3.6*	3.8*	0.86	0.70	2.1
Reared	8.8	Over	Flexed	3.6	3.0	0.48	1.0	0.76	4.1*	4.2*	0.96	0.68	2.6
Reared	11.2	Over	Juv.	4.2	3.7	0.50	1.4	1.1	5.7*	6.0*	1.4	1.0	3.3
Richardson Bay, Calif.	12.9	Over	Juv.	4.5	4.3	0.52	1.2	0.92	7.0*	7.0*	1.5	1.0	3.6
	13.2	Over	Juv.	4.8	4.3	0.75	1.3	1.1	6.7*	7.1*	1.4	1.0	3.6
	14.0	Over	Juv.	5.0	4.7	0.75	1.4	1.2	7.5*	7.7*	1.6	1.2	3.8
	14.5	Over	Juv.	5.2	4.8	0.72	1.4	1.0	7.7*	7.9*	1.8	0.88	4.1
	18.4	Over	Juv.	6.4	5.8	0.80	1.7	1.4	10.0*	10.5*	2.1	1.4	5.1

[1]Sym. - symmetrical; Migr. - migrating.
[2]Str. - straight; E fl. - early flexion; L fl. - late flexion; Juv. - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 17.—Meristics of larvae and juveniles of *Hypsopsetta guttulata*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
7501-120.25	2.8 NL	Prefl.	0	0	0	0	LP[2]				
7501-120.29	3.3	Prefl.	0	0	0	0	LP[2]				
San Diego Bay	3.6	Prefl.	0	0	0	0	LP[2]				
San Diego Bay	4.0	Prefl.	Forming	Forming	Forming	0	LP[2]				
7412-127.32.6	4.4	Prefl.	Forming	Forming	6	0	LP[2]				
7412-127.32.6	4.5	E fl.	Forming	Forming	8	0	LP[2]				
7501-120.22.4	4.9	E fl.	Forming	Forming	6	0	LP[2]				
7501-120.29	5.1	E fl.	Forming	Forming	4	0	LP[2]				
King Harbor, Calif.	5.2	L fl.	ca. 50	ca. 35	15	0	LP[2]				
L.A. Harbor, Calif.	4.4 SL	Postfl.	67	47	19	Bud	LP[2]				
Off La Jolla, Calif.	4.8	Postfl.	66	49	19	Bud	LP[2]				
San Diego Bay	5.4	Postfl.	73	45	19	Bud	LP[2]				
7501-120.22.7	5.9	Postfl.	73	46	19	Bud	LP[2]				
7501-120.24	6.6	Postfl.	69	50	19	6/6	LP[2]				
Reared	7.3	Postfl.	68	47	19	6/6	11/11	11	23	34	X-ray
Reared	7.9	Postfl.	67	51	20	6/6	12/12	12	23	35	X-ray
Reared	8.8	Postfl.	72	50	19	6/6	13/13	12	23	35	X-ray
Reared	11.2	Juv.	73	48	19	4/6	12/12	12	22	34	X-ray
Richardson Bay, Calif.	12.9	Juv.	66	48	19	6/6	12/11	12	23	35	X-ray
	13.2	Juv.	74	53	19	6/6	11/11	12	23	35	X-ray
	14.0	Juv.	78	55	19	6/6	11/11	12	23	35	X-ray
	14.5	Juv.	71	51	19	6/6	12/12	12	23	35	X-ray
	18.4	Juv.	68	51	19	6/6	11/12	12	23	35	X-ray

[1]Prefl. - preflexion; E fl. - early flexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

Postflexion and early transforming specimens are less heavily pigmented than earlier stage larvae, with a noticeable diminution of pigment on the dorsal area of the head and body (Figure 23D).

Morphology.—Larvae of *H. stomata* are closest to *P. coenosus* in size at hatching, notochord flexion, and transformation (Table 18). A specimen 3.7 mm NL has a moderate amount of yolk remaining.

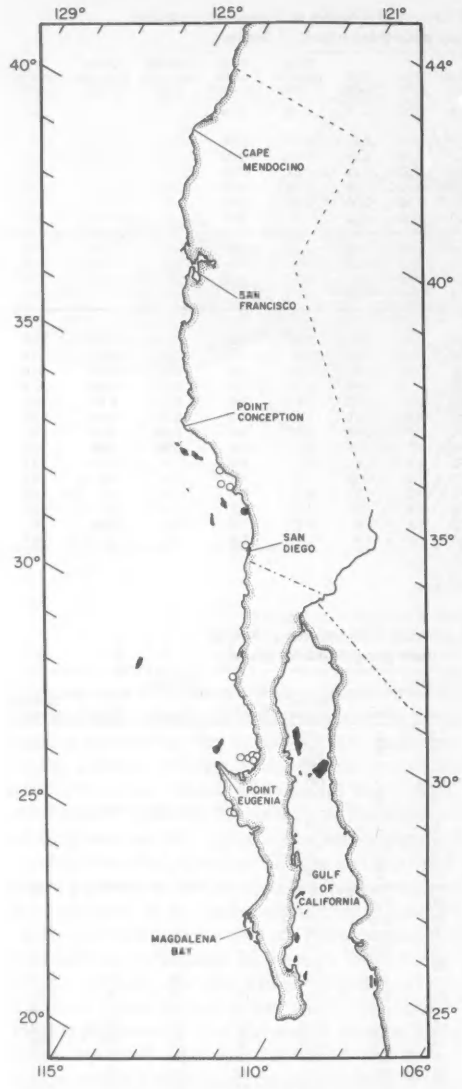


FIGURE 22.—Distribution of eggs and larvae of *Hypsopsetta guttulata* examined in this study. (Open circles represent larvae, closed circles eggs and larvae.)

The right eye is beginning to migrate in a specimen 9.1 mm SL and transformation is almost complete at 11.7 mm SL.

In early preflexion larvae of *Hippoglossina*, the gut is shaped like that in *Pleuronichthys* larvae; however, coiling begins at about 4.5 mm NL and the gut assumes a more compact shape than in *Pleuronichthys*. This is reflected in the relatively shorter snout-anus length. Mean relative snout-anus length remains at about 40% of the body length throughout the larval period, in contrast to *Pleuronichthys* larvae in which there is a gradual decrease in relative gut length during larval development (Table 5). In juveniles, however, there is a decrease in snout-anus length to about 33% of body length, a value comparable with that in *Pleuronichthys* juveniles.

The head is similar in size and shape to that in *Pleuronichthys*. Relative head length increases gradually during larval development. The same is true for relative snout length and is thus opposite to the condition in *Pleuronichthys*; however, it decreases somewhat in juveniles. Relative eye width undergoes a moderate diminution during larval development as in *Pleuronichthys*, but increases moderately in juveniles.

Small preopercular spines develop on larvae from ca. 5.5 mm NL, become most conspicuous on flexion stage larvae, and undergo resorption during transformation from 9.5 mm SL. This spination is distinctive of *H. stomata* when compared with *Pleuronichthys* and *Hypsopsetta*.

Larvae of *Hippoglossina* have a slender appearance compared with some of the deeper bodied species of *Pleuronichthys*. Body depth at the anus is comparatively small in preflexion larvae and remains so in flexion and postflexion larvae and early juveniles (Table 5).

As in *Hypsopsetta*, the caudal peduncle is longer and more slender than in *Pleuronichthys*, except for *P. ocellatus* postflexion larvae.

Fin formation.—Larvae of *Hippoglossina stomata* are comparable with those of *P. coenosus* with regard to size at which the caudal fin develops. Caudal fin formation occurs between 6.2 and 8.8 mm NL (Table 19). Although about six caudal rays are formed on a 7.0-mm NL specimen with a straight notochord, all other specimens with caudal rays have the notochord flexing. The smallest, fully flexed specimen is 7.1 mm SL. Postflexion specimens <9.0 mm SL lack the full complement of 18½ caudal rays. The ural bones supporting the caudal rays are made up of two superior and two inferior hypurals; there is no epural. The lack of an epural bone is a specific

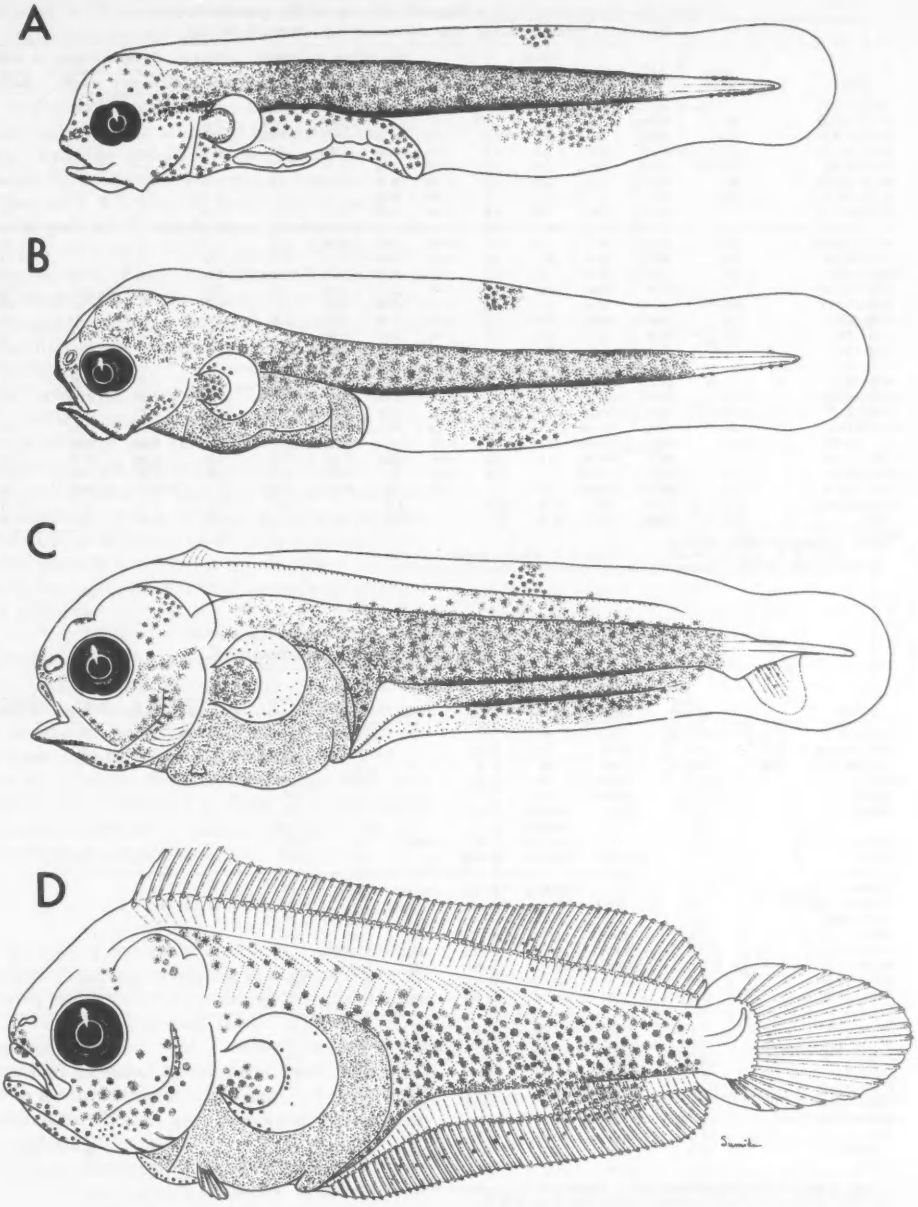


FIGURE 23.—Larval stages of *Hippoglossina stomata*: A. 3.8 mm; B. 4.8 mm; C. 8.3 mm; D. 8.6 mm.

TABLE 18.—Morphometrics, in millimeters, of larvae of *Hippoglossina stomata*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye[1]	Noto-chord[2]	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base[3]	Body depth at anus[3]	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
7201-117.35	3.7 NL	Sym.	Str.	1.4	0.64	0.10	0.28	0.21	0.50	0.40	—	—	—
7412-103.29	4.1	Sym.	Str.	1.8	0.72	0.07	0.24	0.24	0.48	0.36	—	—	—
7412-88.5.31	4.8	Sym.	Str.	2.0	1.0	0.24	0.36	0.28	0.96	0.68	—	—	—
5801-117.35	5.2	Sym.	Str.	2.2	1.2	0.24	0.48	0.36	1.2	0.82	—	—	—
6310-93.28	6.2	Sym.	Str.	2.2	1.3	0.26	0.42	0.36	1.2	0.92	—	—	—
6605-123.37	6.4	Sym.	Str.	2.2	1.3	0.24	0.44	0.36	1.4*	1.0	—	—	—
5910-117.30	6.2	Sym.	Str.	2.8	1.6	0.30	0.54	0.42	2.1*	1.3	—	—	—
6706-110.50	7.0	Sym.	Str.	2.8	1.8	0.32	0.50	0.42	2.1*	1.8*	—	—	—
5708-118.5.35	6.6	Sym.	E fl.	2.7	1.7	0.40	0.54	0.54	2.1*	1.7*	—	—	1.5
5706-127.34	7.5	Sym.	E fl.	3.0	2.0	0.36	0.66	0.70	2.2*	1.8*	—	—	1.8
6912-83.60	8.3	Sym.	E fl.	3.2	1.8	0.42	0.60	0.66	2.4*	2.0*	—	—	2.0
5807-130.30	7.6	Sym.	Midfl.	2.9	1.9	0.38	0.64	0.58	2.2*	2.0*	—	—	1.8
5709-110.30	7.9	Sym.	Midfl.	2.9	1.9	0.42	0.60	0.52	2.2*	2.0*	—	—	1.7
6706-123.37	8.8	Sym.	Midfl.	3.4	2.3	0.44	0.68	0.60	2.8*	2.4*	—	—	2.4
5706-123.37	7.6	Sym.	L fl.	3.1	2.1	0.46	0.66	0.64	2.5*	2.3*	—	—	1.8
6706-123.36	8.5	Sym.	L fl.	3.4	2.3	0.44	0.70	0.66	2.8*	2.6*	—	—	2.3
6608-120.30	7.1 SL	Sym.	Flexed	3.1	2.2	0.46	0.76	0.78	2.6*	2.4*	0.66	0.62	2.1
5708-115.35	8.0	Sym.	Flexed	3.3	2.4	0.64	0.72	0.68	2.9*	2.7*	0.62	0.70	2.0
6706-123.37	9.0	Sym.	Flexed	3.9	2.7	0.52	0.84	0.84	3.4*	3.0*	0.70	0.82	2.7
6410-83.43	9.4	Sym.	Flexed	3.7	2.7	0.56	0.84	0.84	3.6*	3.8*	0.80	0.84	2.3
5701-120.35	9.1	Migr.	Flexed	3.8	3.1	0.72	1.0	0.96	3.7*	4.1*	0.92	0.68	2.7
5709-110.33	9.9	Migr.	Flexed	4.0	3.2	0.80	0.90	0.86	4.1*	4.3*	0.90	0.76	2.6
6706-123.36	10.5	Migr.	Flexed	4.1	3.5	0.80	1.1	0.94	3.8*	3.9*	0.98	0.88	3.0
5507-130.30	11.7	Migr.	Flexed	4.2	3.7	0.96	1.0	0.88	4.4*	4.5*	1.2	0.90	3.5
Asuncion Bay, B.C.	35.8 38.2	Over Over	Juv. Juv.	12.4 12.2	12.2 13.5	2.3 2.7	4.3 4.2	— —	13.4* 14.2*	13.0* 13.7*	3.2 3.8	2.9 3.4	10.5 11.4

[1]Sym. - symmetrical; Migr. - migrating.
[2]Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.
[3]Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 19.—Meristics of larvae and juveniles of *Hippoglossina stomata*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage[1]	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
7201-117.35	3.7 NL	Prefl.	0	0	0	0	LP[2]				
7412-103.29	4.1	Prefl.	0	0	0	0	LP[2]				
7412-88.5.31	4.8	Prefl.	0	0	0	0	LP[2]				
5801-117.35	5.2	Prefl.	0	0	0	0	LP[2]				
6310-93.28	6.2	Prefl.	0	0	0	0	LP[2]				
6605-123.37	6.4	Prefl.	Anterior swelling	0	0	0	LP[2]				
5910-117.30	6.2	Prefl.	Forming	0	Forming	0	LP[2]				
6706-110.50	7.0	Prefl.	Forming	Forming	ca. 6	0	LP[2]				
5708-118.5.35	6.6	E fl.	Forming	Forming	ca. 6	Bud	LP[2]				
5706-127.34	7.5	E fl.	Forming	Forming	ca. 10	Bud	LP[2]				
6912-83.60	8.3	E fl.	Ant. 4	Forming	ca. 10	Bud	LP[2]				
5807-130.30	7.6	Midfl.	ca. 15	ca. 15	12	Bud	LP[2]				
5709-110.30	7.9	Midfl.	ca. 55	ca. 45	12	Bud	LP[2]				
6706-123.37	8.8	Midfl.	ca. 62	ca. 50	16	Bud	LP[2]				
5706-123.36	7.6	L fl.	ca. 63	ca. 45	14	Bud	LP[2]				
6706-123.36	8.5	L fl.	ca. 68	ca. 50	14	Bud	LP[2]				
6608-120.30	7.1 SL	Postfl.	ca. 66	ca. 51	16	ca. 5/5	LP[2]				
5708-115.35	8.0	Postfl.	63	50	ca. 18	6/6	LP[2]				
6706-123.37	9.0	Postfl.	68	53	18½	5/5	LP[2]				
6410-83.43	9.4	Postfl.	68	54	ca. 18	6/6	LP[2]				
5701-120.35	9.1	Postfl.	67	53	18½	6/6	LP[2]				
5709-110.33	9.9	Postfl.	65	50	18½	6/6	LP[2]				
6706-123.36	10.5	Postfl.	66	53	18½	6/6	LP[2]				
5507-130.30	11.7	Postfl.	64	50	18½	6/6	LP[2]				
Asuncion Bay, B.C.	35.8 38.2	Juv. Juv.	67 65	52 50	18½ 17½	6/6 6/6	10/10 10/10	11 11	27 27	38 38	X-ray X-ray

[1]Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.
[2]LP refers to functional larval pectoral fins which have no ossified rays.

character in *H. stomata* because other species of *Hippoglossina* possess this bone.

The dorsal fin of *H. stomata* develops quite differently than in *Pleuronichthys*. An anterior group of about five dorsal rays is the first to form in *H. stomata*; these become more elongated than the other rays. The anlage of these is evident on a 6.4-mm NL preflexion specimen and four rays are formed on a 9.3-mm NL early flexion larva. A similar pattern of early forming dorsal fin rays is found in the closely related genera *Paralichthys* (Okiyama 1967; Smith and Fahay 1970; Ahlstrom and Moser 1975) and *Pseudorhombus* (Devi 1969). Although the anterior dorsal rays form early, the pelvic fins do not develop elongated rays, such as in the bothid genera *Syacium* (Aboussouan 1968) and *Cyclopsetta* (Gutherz 1970). The dorsal fin rays differentiate posteriad but most rays form simultaneously and the full complement is developed on a late flexion specimen. The base of the anal fin is evident during early caudal formation, rays are forming on midflexion specimens, and the total number is formed on a late flexion specimen. Pelvic fin buds are evident on early flexion specimens, but rays can be distinguished only on postflexion larvae.

Distribution.—This species ranges from Monterey Bay, Calif., to the Gulf of California, including Guadalupe Island (Miller and Lea 1972). Larvae occurred over a wide band of inshore and offshore stations (Figure 24). The southern limit of *H. stomata* overlaps the northern range of *H. tetrophthalmus* which has different fin counts (Ginsburg 1952). To date, larvae of *H. tetrophthalmus* are not known.

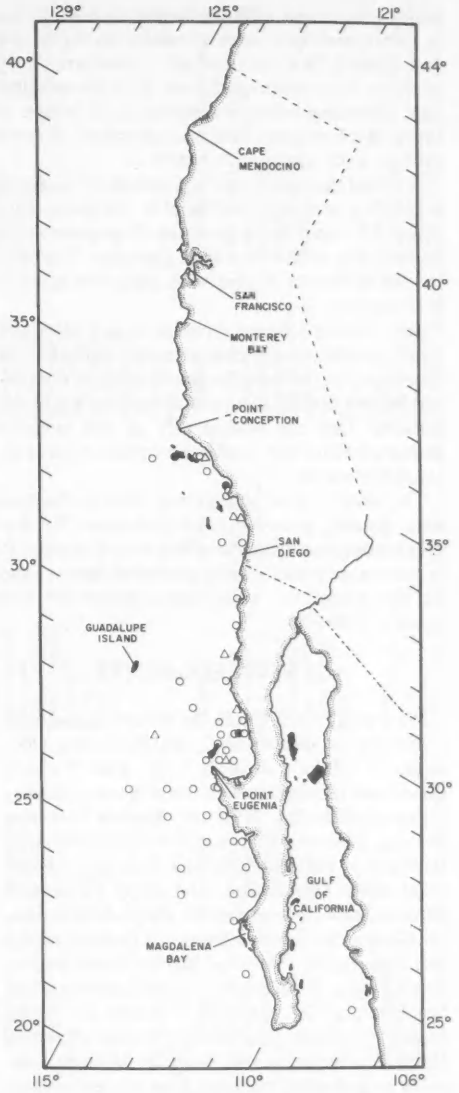


FIGURE 24.—Distribution of eggs and larvae of *Hippoglossina stomata* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

SUMMARY

We used a combination of larval morphology, meristics, and pigmentation to distinguish seven known eastern North Pacific species of flatfishes with heavily pigmented larvae. Table 20 summarizes many pertinent characters for identifying eggs and larvae of these species. Information is given for three characters of eggs: size, ornamentation of the chorion, and presence or absence of an oil globule.

In most instances, the size of a newly hatched larva is directly related to the size of the egg from which it hatched, and such is the case with *Pleuronichthys*. *Pleuronichthys decurrens*, with the largest egg, has the largest larva, with a successive decrease in larval size of the other species corresponding to their smaller sized eggs. This also applies to the yolk-sac larvae of *Hypsopsetta guttulata* and *Hippoglossina stomata*. *Pleuron-*

ichthys decurrens, with the largest yolk-sac larva, is correspondingly large at caudal fin formation (notochord flexion) and at transformation, whereas *Hypsopsetta guttulata*, with the smallest egg, is correspondingly smallest at all stages of larval development with the exception of some overlap with larvae of *P. ritteri*.

A larval character that is particularly useful in separating preflexion larvae of *H. guttulata* from those of *P. ritteri* is the presence of a pterotic spine on each side of the head of *H. guttulata*. The only species of *Pleuronichthys* with a pterotic spine is *P. decurrens*.

For relating a larval series to its juveniles and adults, and thus substantiating identification of the series, meristic counts, particularly of the precaudal and caudal groups of vertebrae, are indispensible. One can seldom rely on one meristic character alone, but must use a combination of all available counts.

The distribution of pigment, which changes with growth, provides good characters for discriminating among larvae of the several species. It is particularly useful with preflexion larvae, and for this reason we emphasize pigment for this stage in Table 20.

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TABLE 20.—Summary of egg and larval characters useful in identifying flatfishes with heavily pigmented larvae.

Characters	*Pleuronichthys decurrens*	*P. coenosus*	*P. verticalis*	*P. ocellatus*	*P. ritteri*	*Hypsopsetta guttulata*	*Hippoglossina stomata*
Eggs:							
Diameter	1.84-2.08	1.20-1.56	1.00-1.16	No data	0.94-1.08	0.78-0.89	1.22-1.38
Chorion	Polygonal sculpturing	Polygonal	Polygonal		Polygonal	Smooth	Smooth
Oil globule	0	0	0		1 (0.10 mm)	1 (0.13 mm)	1 (0.23 mm)
Larval morphology:							
Size of available yolk-sac larvae (mm NL)	4.9 (5.54-Budd 1940)	3.9 (3.88-Budd 1940)	2.4 (3.16-Budd 1940)	No data	2.1	2.2-2.3 (1.7-2.1-Eldridge 1975)	3.7
Size range of preflexion larvae	4.9-9.8	3.7-8.5	2.4-5.8	No data	2.1-5.1	2.2-4.4	3.7-7.0
Size range at caudal fin formation (mm NL)	7.8-11.0	6.2-8.5	5.0-7.2	No data <6.6	4.3-5.6	4.0-5.2	6.2-8.8
Size range during transformation (mm SL)	10.5-<29.4	8.2-<17.0	7.3-<12.2	No data	6.0-<12.7	4.4-<11.2	9.1->11.7
Pterotic spines	1 on each side	0	0	0	0	1 on each side	0
Elongated anterior dorsal rays	0	0	0	0	0	0	ca. 5
Meristics:							
Precaudal vertebrae	14-15 (14)	12-13 (13)	13	12-13 (12)	12-13 (12)	11-12 (12)	11
Caudal vertebrae	24-26 (25)	24-26 (24-25)	22-25 (23)	22-24 (22-23)	22-24 (23)	22-24 (23)	26-28 (27)
Caudal rays	18-20 (19)	19-21 (19)	19	18-19 (19)	19-20 (19)	19-20 (19)	17½-18½ (18½)
Pigmentation:							
Finfold of early larvae	Entirely pigmented except for extreme posterior portion of tail	Opposing clusters approx. midway on tail region	Triangular cluster behind anus ventrally; dorsal cluster slightly forward of ventral cluster; persist through notochordal flexion	No data	Few scattered melanophores on distal margins near anus; these do not persist after long preservation. Often with expansion of melanophores along both margins of body posterior to anus	Opposing pigment extending from body posterior of the anus	Small rounded patch dorsally and broad patch ventrally from middle part of tail
Top of head to shoulder region in early larvae	Present	Present	Absent	No data	Absent	Present	Present but sparse
Unpigmented posterior tail region	Extreme tip of notochord only in very early larvae	Tip of notochord followed by narrow posterior band of caudal peduncle in later stages	Last 3 to 5 myomeres through early notochordal flexion, followed by unpigmented caudal peduncle (shorter than in *P. ritteri*)	Caudal peduncle in late larvae	Last 7 or 8 myomeres through notochordal flexion; entire caudal peduncle unpigmented where dorsal & anal fins terminate in transforming sizes	Last 9 to 10 myomeres prior to notochord flexion shortening to 5 or 6 myomeres after flexion	Tip of tail
Pectoral fin base or fin membrane prior to caudal fin formation	Few melanophores scattered on fin base	None	None	No data	Small melanophores along proximal margin of fin membrane	Two to three melanophores on fin base, particularly at symphysis	Dense pigment on fin base, sparse on fin membrane

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ASSOCIATIONS OF TUNA WITH FLOTSAM IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

The fishing record for flotsam-associated tuna in the eastern tropical Pacific was examined. The rivers of Central America are probably the major source of flotsam. Correlation analysis of the number of sets occurring in an area indicates that unassociated tuna and flotsam-associated tuna are related. The number of sets made on floating objects has increased dramatically since 1971. The percentage of flotsam-associated sets has increased, indicating that flotsam-associated sets are more important to the tuna fishery than in 1963. The catch per set of tuna associated with flotsam has also increased markedly since 1967. Analysis of length-frequency data indicate that, on a single set basis, tuna fork length is more variable in sets associated with flotsam than with unassociated schoolfish sets. Results of the length-frequency analysis support the idea that flotsam aggregates tuna.

The catch of the eastern tropical Pacific tuna fishery consists of mostly yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*. The catch is frequently categorized by the conditions under which the purse seine set is made. Scott (1969) made a major distinction between associated schools and unassociated schools. Associated schools are caught either in "porpoise sets" (sets associated with porpoise) or "floating object sets" (sets associated with logs or other flotsam). Unassociated schools are caught in "night sets" (sets made at night with the aid of bioluminescence) and "schoolfish sets" (schools seen and set upon during the day). Night sets compose a very small proportion of total sets and will not be discussed in this paper. Porpoise sets catch mostly yellowfin tuna. Floating object sets and schoolfish sets catch yellowfin and skipjack tuna, either as pure or mixed species.

Little is known about the attraction of tuna to flotsam. Gooding and Magnuson (1967) and Hunter and Mitchell (1968) observed fish gathering around flotsam. These authors attracted some tuna to their flotsam, but never large schools. Tuna were a minor portion of the observed fish assemblages. Hunter and Mitchell (1968) postulated a connection between schooling behavior and the attraction of fish to flotsam. They concluded that flotsam had the function of providing (p. 27) " . . . a visual stimulus in an optical void." Gooding and Magnuson (1967) concluded that fish gathered around floating objects at sea primarily because the objects provided shelter from predation. It may be possible that the same factors attracting smaller fish also attract large tuna schools.

This paper examines historical tuna fishery data on the catches of yellowfin and skipjack tuna associated with floating objects in the eastern tropical Pacific from 1963 to 1975. The objectives of the paper are to 1) establish the main sources of flotsam, 2) determine if there is a connection between various set types, 3) see if flotsam-associated sets have become more important to the tuna fishery, 4) determine if the catch rate on flotsam-associated sets has changed, and 5) assess whether flotsam does aggregate tuna schools.

METHODS

Since the catch of tuna associated with flotsam depends on the presence of tuna, flotsam, fishermen, strength of attraction, and suitable fishing conditions, I examined each factor in light of the published literature and available fishery data from the eastern tropical Pacific tuna fishery.

The Inter-American Tropical Tuna Commission (IATTC) collects information from tuna fishermen operating in the eastern tropical Pacific. Information collected in logbooks includes date and location of sets, catch of various species, type of set, and environmental conditions. Although these logbooks remain confidential, it is possible to obtain summaries of the information for certain time-area strata. During the beginning portion of

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the year, yellowfin tuna fishing is unregulated. After a quota is reached (Table 1), all yellowfin tuna fishing, except for special allowances must be outside the Commission's Yellowfin Regulatory Area (CYRA) (Figure 1). Due to special rules (see Inter-American Tropical Tuna Commission 1967-1975), any detailed reporting of regulated data would compromise the confidentiality of the data; hence, only unregulated catch and number of sets within the CYRA summarized by month and 5° square for 1963-75 were made available to me.

TABLE 1.—Yellowfin quota (thousands of short and metric tons), closure data, and annual total catch (thousands of short and metric tons) for the Commission's Yellowfin Regulatory Area, taken from Calkins (1976).[1] Metric tons are given in parentheses.

Year	Quota	Quota + increment[2]	Closure date	Annual total catch
1966	79.3 (71.9)		Sept. 15	91.1 (82.6)
1967	84.5 (76.6)		June 24	89.6 (81.3)
1968	106.0 (96.1)		June 18	114.6 (103.9)
1969	120.0 (108.8)		Apr. 16	126.5 (114.7)
1970	120.0 (108.8)		Mar. 23	142.6 (129.3)
1971	140.0 (127.0)		Apr. 9	113.9 (103.3)
1972	120.0 (108.8)	140.0 (127.0)	Mar. 5	152.5 (138.3)
1973	130.0 (117.9)	160.0 (145.1)	Mar. 8	177.8 (161.3)
1974	175.0 (158.7)	195.0 (176.9)	Mar. 18	191.3 (173.5)
1975	175.0 (158.7)	195.0 (176.9)	Mar. 13	177.2 (160.7)
1976	175.0 (158.7)	195.0 (176.9)	Mar. 27	205.5 (186.4)

[1]Calkins, T. P. 1976. The 1976 fishing year (through August 30). Background Paper No. 1, 33rd meeting of the Inter-American Tropical Tuna Commission.

[2]The Director of IATTC may increment the established quota, allowing more yellowfin tuna to be caught.

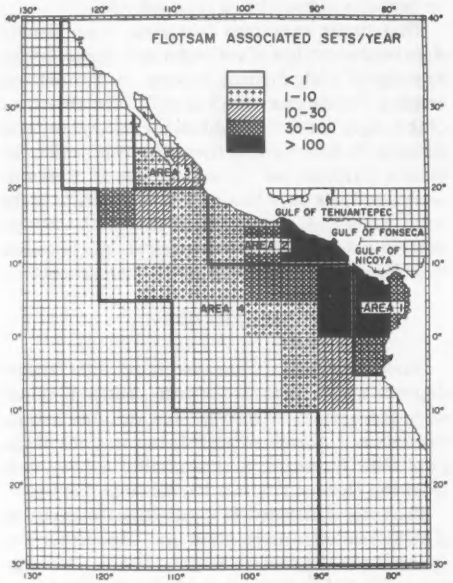

FIGURE 1.—Eastern tropical Pacific fishing area divided into three nearshore areas (Areas 1-3) and one offshore area (Area 4). The heavy line to the west delimits the boundary for the Commission Yellowfin Area (CYRA). The average number of flotsam-associated sets from 1972 to 1975 by 5° squares is shown. Data represent the unregulated fishing period (see text).

The total number of unregulated sets during the 13 yr was approximately 161,000 of which 8,190 were associated with flotsam. In addition, the IATTC provided the total number of flotsam-associated sets occurring each year (Figure 2). One sees that the major trends in the number of sets are contained in the block of unregulated data.

NOAA's Southwest Fisheries Center (SWFC) periodically sends technicians aboard tuna seiners. These technicians record details about set type, catch, environmental conditions, as well as the fork length (centimeters) of tuna sampled from individual sets. Fork lengths of yellowfin and skipjack tuna were only available for a limited number of sets made in 1973-75. The location of fork length measurements are given in Table 2. Single set catch data were collected by SWFC technicians in 1974-76 (unpubl. data[2]).

[2]Unpubl. data on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

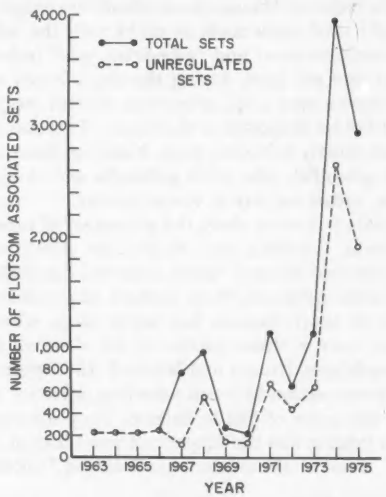

FIGURE 2.—Total number of flotsam-associated sets made in the eastern Pacific and number of unregulated flotsam-associated sets made in the CYRA, 1963-75.

TABLE 2.—Spatial distribution of fork length measurement (centimeters) of yellowfin and skipjack tuna in the Commission's Yellowfin Regulatory Area, 1973-75. CYRA subareas are shown in Figure 1. (Source of data, SWFC.)

CYRA subarea	Number of sets where fork length was measured
1	56
2	12
3	14
4	29

Monthly rainfall in Central America was calculated by averaging the stations reporting to the Environmental Data Service (U.S. Department of Commerce 1963-1975).

In order to achieve the objectives of this paper, the data obtained from IATTC and SWFC were examined and analyzed in several ways. The main sources of flotsam were inferred by examining the average distribution of flotsam-associated sets and consideration of the average surface circulation.

Two methods may be used to determine if different set types are related: correlation of set types occurring in an area and comparison of fork length distributions (length-frequency graphs) stratified by species and set type. Spearman's rank correlation coefficient (Siegel 1956) was calculated to expose possible correlations of numbers of sets. Fork length distributions were weighted by the catch in each set. A high positive correlation between set types occuring in an area would indicate a relationship between set types. Similar looking length-frequency distributions would serve as further evidence that set types are related.

An increase in the percentage of flotsam-associated sets would be evidence that flotsam-associated sets have become more important to the fishery. The CYRA was subdivided into three nearshore areas and one offshore area (Figure 1). Stratifying the number of flotsam-associated sets by area allows the determination of area effects. Hence, the importance of flotsam to the fishing industry may be determined by the percentage of flotsam-associated sets occurring each year and stratifying the number of flotsam-associated sets by area.

Average rainfall was tabulated to determine if any connection existed between river runoff and the number of flotsam-associated sets.

Catch rate is an indicator of the importance of flotsam-associated sets to the tuna fishery. Calculation of the average yearly catch per set (including zero catch sets) for different set types should demonstrate any trends as well as the relative value of making one set type over another.

Calkins (1965) examined tuna length distributions from single sets in the eastern tropical Pacific, finding that single unassociated schoolfish sets caught tuna of a relatively uniform size (i.e., small variance in length). If the fish caught in flotsam-associated sets represent aggregations of solitary tuna, portions of schools, or several schools, then one would expect the variance of tuna length to be greater than for unassociated schools. In order to examine if floating objects act as aggregators, length-frequency data were stratified by species and set type. Mean length and standard deviation were calculated on a single set basis for each category and compared using Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956).

If flotsam does aggregate tuna, one would expect more of the larger flotsam-associated sets than unassociated sets. Differences in catch distribution were observed by plotting histograms of tons of tuna caught per set stratified by year and set type and by calculating catch per successful set for each year and set type. The single set catch data, collected by SWFC technicians, existed for the 1974-76 period.

RESULTS

The availability of logs or other flotsam in an area are determined by the source of the flotsam and the currents in the area. Large rivers flow into the Pacific from southern Mexico (lat. 20°N) and continue down the coast of South America (to lat. 20°S). These rivers are capable of releasing many logs into the Pacific during the rainy season. SWFC and IATTC observers reported large densities of logs near the Gulf of Tehuantepec (lat. 16°N, long. 100°W), the Gulf of Nicoya (lat. 10°N, long. 85°W), and the Gulf of Fonseca (lat. 13°N, long. 87°W).

The average yearly number of flotsam-associated sets in 1972-75 were plotted by 5° squares (Figure 1). In general, most flotsam-associated sets occurred in Areas 1 and 2. Most of the offshore flotsam-associated sets (i.e., Area 4) occurred quite close to Areas 1 and 2. Area 3 did not have large numbers of flotsam-associated sets. If the main source of logs and other flotsam is the rivers of Central America, then it is important to examine the major current patterns in the eastern tropical Pacific to determine if the currents can

explain the observed distribution of flotsam-associated sets.

The average currents in the eastern tropical Pacific, as derived from ship's drift data, were determined by Wyrtki (1965). From January until May, the California Current is strong. Circulation near Area 3 is to the south. Circulation near Areas 1 and 2 is gyral. From May to July, both the Equatorial Countercurrent and the California Current are relatively stong. During this period, most countercurrent water turns north and flows along the coast of Central America. Area 3 has a northern and southern flow, the northern flow along the coast. Area 1 maintains its gyral flow. From August through December, the Equatorial Countercurrent is well developed. Circulation in Area 3 is to the south. Area 2 maintains its northwestern flow along the coast and Area 1 flow maintains a gyral pattern. If logs disperse mainly from the Gulf of Nicoya, the Gulf of Tehuantepec, and the Gulf of Fonseca, then the gyral circulation in Area 1 would tend to maintain logs and other flotsam in the area for a considerable time. The northwest coastal current in Area 2 could transport flotsam through Area 2 and during part of the year into Area 3. Since the North Equatorial and South Equatorial Currents are rather strong, one would not expect floating objects to persist in Area 4 except near the boundaries with Areas 1 and 2. Hence the location of large rivers and the system of currents is reasonably consistent with the geographical distribution of flotsam-associated sets.

In order to compare different set types, Spearman's rank correlation coefficient was calculated. For each 5° square in the CYRA, the total numbers of flotsam-associated sets, porpoise-associated sets, and unassociated schoolfish sets were tabulated for each year. These totals were ranked and the ranks were correlated. Only 5° squares where at least 10 sets occurred were used in calculating correlations. When a minimum of 40 sets was used as the criterion for including a 5° square, the correlations were qualitatively the same as with the 10 sets criterion. The results (Table 3) show that a significant positive correlation exists between number of sets on unassociated schoolfish and flotsam-associated tuna. Porpoise sets were uncorrelated with other set types.

The above results indicate that fish caught associated with flotsam tended to be caught in the same area at the same time as unassociated school fish. Examination of available length-frequency data on a species basis, weighted by the catch in each set (Figure 3), indicated that unassociated schoolfish and flotsam-associated yellowfin and skipjack tuna had very similar length-frequency distributions. The length-frequency information and the correlation analysis support the idea that unassociated tuna and flotsam-associated tuna are related. Flotsam, acting as an attractant, may aggregate tuna that would otherwise be caught in unassociated sets.

TABLE 3.—Spearmans rank correlation between three types of sets by year. Number of sets/5° square. (Source of data: IATTC.)

Year	N	Unassociated schoolfish and porpoise-associated	Unassociated schoolfish and flotsam-associated	Porpoise and flotsam-associated
1963	29	-0.0008	0.5421**	0.2538
1964	27	0.0375	0.1581	0.8138**
1965	25	-0.1597	0.3498*	0.1318
1966	28	-0.1110	0.3513*	0.2914
1967	24	-9.2379	0.4621*	-0.2255
1968	24	-0.1951	0.1886	0.3463*
1969	25	-0.1523	0.5957**	0.2294
1970	27	-0.0088	0.3529*	-0.0173
1971	26	0.0803	0.5819**	0.2398
1972	32	-0.0200	0.5277**	-0.0558
1973	34	0.0523	0.3086*	0.1796
1974	27	0.0168	0.4847**	0.0001
1975	33	0.2444	0.5139**	0.0526

*Significant at $P \leq 0.05$.
**Significant at $P \leq 0.01$.

The number of flotsam-associated sets has increased dramatically since 1971 (Figure 2). The trend in percentage of flotsam-associated sets (Figure 4) indicates that flotsam-associated sets have increased in importance to the fishery. Stratifying the number of unregulated flotsam-associated sets by area (Figure 5) shows that the trend of more flotsam-associated sets is not an area effect. All areas, except Area 3, have shown a marked increase in number of flotsam-associated sets. Area 3 does not show an increase because logs are only deposited in this region during a limited portion of the year. In January-May, the near surface current in Area 3 is to the south (Wyrtki 1965), cutting off the source of logs that wash down the rivers of Central America. Also, good fishing often occurs in Area 3 during the later months of the year, a period not included in my unregulated data. It appears that the increase in flotsam-associated sets in recent years was not caused by discovery of new areas with abundant flotsam but rather by an increase in fishing effort on flotsam in all areas but Area 3.

Average rainfall in Central America was tabulated (Table 4) to see if there was a correlation between river runoff and the number of flotsam-associated sets. Comparison of number of flotsam-associated sets and rainfall revealed only

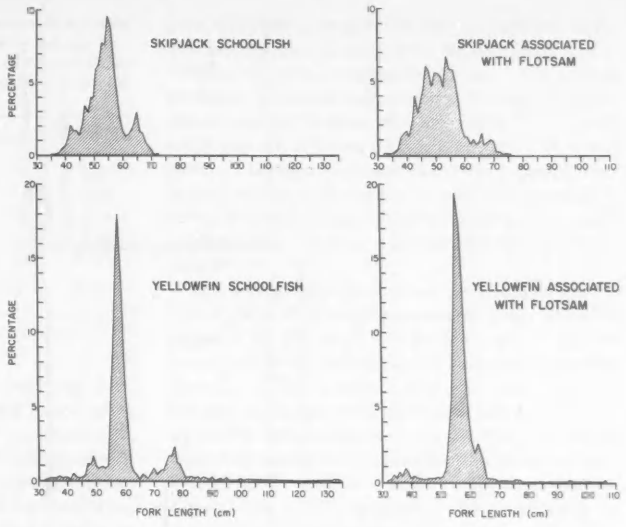

FIGURE 3.—Length-frequency distributions of yellowfin and skipjack tuna caught in unassociated schoolfish and flotsam-associated sets. Data collected 1973-75 in the CYRA (see Table 2).

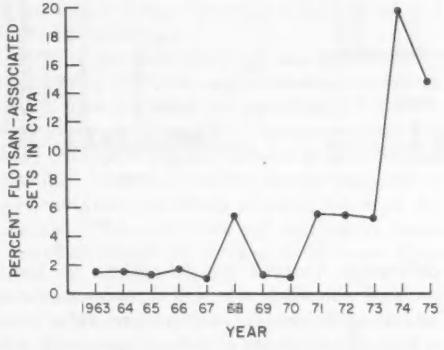

FIGURE 4.—Percentage of total unregulated sets that were associated with flotsam in the CYRA, 1963-75.

small similarities, indicating that the supply of suitable flotsam was not greatly influenced by rainfall.

Comparing the average catch per set of different set types indicates the relative importance of each set type to the fishery as well as showing trends in the catch rate (Figure 6). All set types had similar catch rates in 1963-66. Porpoise sets and flotsam-associated sets gave much higher catch per set than unassociated sets in 1971-75. One sees that flotsam-associated sets have been the most valuable set type for the tuna fisherman since 1971.

TABLE 4.—Average yearly rainfall (centimeters) in Central America in 1963-75. (Source: U.S. Department of Commerce.)

Year	Average yearly rainfall	Year	Average yearly rainfall
1963	139.0	1970	163.8
1964	136.4	1971	145.5
1965	136.9	1972	145.6
1966	158.5	1973	161.4
1967	151.7	1974	172.3
1968	177.3	1975	151.0
1969	177.2		

Fork length data was stratified by set type and species. The mean length, standard deviation, and sample size were calculated on a single set basis (Table 5). The average standard deviation of fork length of yellowfin and skipjack tuna associated with flotsam was larger than the standard deviation found in unassociated sets, though the mean fork length of flotsam-associated sets was smaller. The probability of getting the results shown (Table 5) by chance was calculated using Kruskal-Wallis one-way analysis of variance (Siegel 1956:184) (Table 5). The greater variability of fork length of flotsam-associated tuna supports the hypothesis that flotsam aggregates tuna.

The yellowfin and skipjack tuna catch distribution on flotsam-associated sets was compared with unassociated schoolfish sets. The average catch per successful set was calculated and the data were plotted as histograms of tonnages using an arbitrary interval of 5 tons (Figure 7). The main

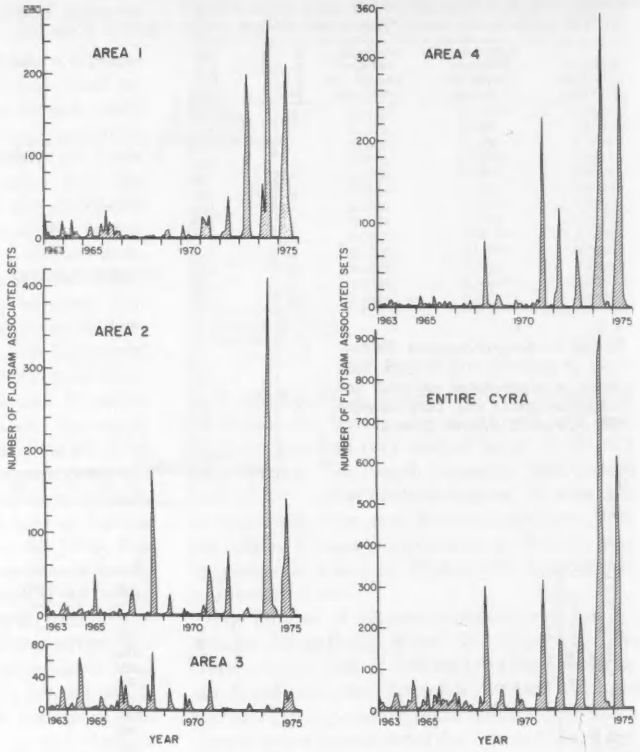

FIGURE 5.—Number of unregulated flotsam-associated sets per month by area, 1963-75.

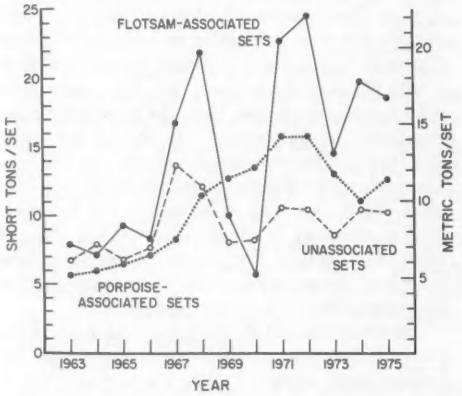

FIGURE 6.—Average yearly catch per set of yellowfin and skipjack tuna in flotsam-associated, unassociated schoolfish, and porpoise-associated sets in the CYRA.

differences between the histograms for unassociated schoolfish sets and flotsam-associated sets are a lower proportion of unsuccessful sets and a higher percentage of flotsam-associated sets with catches between 25 and about 60 tons. The higher proportion of large flotsam-associated sets is consistent with the hypothesis that flotsam aggregates tuna.

DISCUSSION

Changes in catch rate (catch per set, Figure 6) of flotsam-associated yellowfin or skipjack tuna may be related to overall abundance of flotsam-associated schools, technological advances such as bigger nets, increased skill and knowledge of the fishermen, changes of the attractability of flotsam, and changes in the residence time of tuna with flotsam. In order to explain the observed increase

TABLE 5.—Variability of fork length (centimeters) in single set data by tuna species and set type, as indicated by average standard devation ($\bar{S}$) and mean ($\bar{x}$) and results of Kruskal-Wallis one-way analysis of variance of standard deviations. (Source of data: SWFC.)

Item	Yellowfin tuna	Skipjack tuna
Flotsam-associated sets:		
N	35	45
$\bar{S}$	4.96	4.62
$\bar{x}$	55.55	52.49
Unassociated schoolfish:		
N	49	43
$\bar{S}$	3.76	3.40
$\bar{x}$	60.94	54.08
Kruskal-Wallis:		
H	3.69	33.31
df	1	1
Probability level	$0.05 \leq P \leq 0.1$	$P \leq 0.001$

in catch rate, it was necessary to examine data that could indicate which factors have most influenced catch rate. Changes in attractability, changes in residence time, technological advances, and increased knowledge of the fisherman could not be rejected or confirmed with existing data. It was possible, with some assumptions, to determine if overall abundance changes or increased skill of the fisherman could explain the increased catch rate.

If the overall abundance of tuna had increased from 1963 to 1975, then one would expect the catch rate to have increased correspondingly. If one accepts the supposition that flotsam-associated fish were from the same population as unassociated schoolfish, then one would expect the catch rate on unassociated schoolfish to have likewise increased. The catch per set on unassociated schoolfish (Figure 6) showed no increase. However, the year-to-year variations in catch per set of flotsam-associated tuna and unassociated tuna (Figure 6) were remarkably similar. The above evidence indicates that changes in overall abundance does not explain the long-term increase of catch per set in flotsam-associated sets. The similarity of the year-to-year variations supports the hypothesized relationship between unassociated schoolfish and flotsam-associated tuna. The year-to-year variation may represent changes of abundance.

The second explanation for the changes in the catch rate of flotsam-associated tuna schools, changes in the skill of the fisherman, can be evaluated by the percentage of successful sets. An increase in the percentage of successful sets on schools associated with flotsam would explain the apparent increase in catch per set. Such an explanation is untenable because the percentage of successful sets would have had to more than double. Greenblatt (1977) calculated the percentage of successful sets associated with flotsam for 1974-76, finding the average percentage of successful sets to be 75%. To account for the change in catch/set, the percentage of successful sets in 1963 would have had to have been about 35%, an unreasonably low figure. Pella and Psaropulos (1975, fig. 2) showed that the percentage of successful sets of unassociated schoolfish sets and flotsam-associated sets (considered as one category) did not increase enough in 1961-71 to account for the observed changes in catch per set. Bayliff and Orange (1967) reported percentages of successful sets stratified by set type for a limited area of the

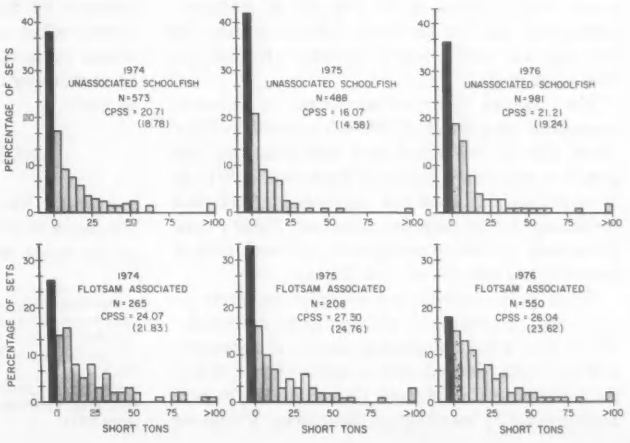

FIGURE 7.—Distribution of catch by 5 short ton intervals for flotsam-associated sets and unassociated schoolfish from 1974 through 1976. Solid boxes indicate percentage of zero catch sets. The average catch per successful set (CPSS) in short and metric tons is given for each category. Metric tons are in parentheses.

CYRA. Although they had small numbers of sets, the percentage of successful flotsam-associated sets from 1962 to 1966 was 67.6%. Changes in percentage of successful sets can not adequately explain the increased catch per set.

No satisfactory explanation for the increase in catch per flotsam-associated set has been found. Overall increases in abundance or increased skill of the fishermen can not explain the increase. The above factors may account for some of the increase. Technological advances may account for the increased catch rate. It is also reasonable to believe that fishermen have learned to catch flotsam-associated tuna more efficiently and the residence time of tuna with flotsam has increased since 1967.

Changes in catch per set on flotsam-associated sets may have been due to technological advances such as bigger nets. If technological advances can explain the increased catch per set on flotsam, then either the catch per set on unassociated schoolfish should have also increased or sets associated with flotsam prior to the technological advances must have caught a low proportion of potential catch. Nets have increased in size, perhaps increasing the probability of catching yellowfin and skipjack tuna which may aggregate around flotsam. It is possible that bigger nets could account for increased catch/set of flotsam-associated sets without likewise affecting catch/set on unassociated schoolfish sets.

Fishermen often will drift with logs for considerable time, waiting for tuna aggregations to reach an optimal size before setting the net. The spread of such behavior throughout the fleet could cause the overall catch per set of flotsam-associated tuna to increase. Adequate data for testing this "increased knowledge" hypothesis was unavailable.

The marked changes occurring in flotsam-associated tuna catch in 1963-75 coincided with a large increase of effort and technology in the porpoise-associated fishery (Green et al. 1971). It is hypothesized that the increased effort and technology in the porpoise-associated fishery may have been related to changes in the catch rate of tuna schools associated with flotsam.

When purse seiners set on porpoise, there is often an incidental kill of the marine mammals. Due to recent technological advances, the porpoise kill has been reduced, but in earlier years of the porpoise-associated fishery (the mid-1960's) porpoise mortality was higher (Southwest Fisheries Center[3]). This incidental kill may have reduced the porpoise population. The porpoise-associated fishery first developed near shore and thus the nearshore porpoise stocks have been affected for a longer time than offshore stocks. One may reasonably speculate that, on a species basis, nearshore porpoise stocks have been affected more by incidental kills than offshore porpoise stocks.

The bond between tuna and porpoise is not understood. It is possible that the mechanisms involved in the association of tuna with porpoise is similar to those responsible for their association with flotsam. Tuna associated with flotsam are, on the average, smaller than tuna associated with porpoise (Calkins 1965, tables 2 and 9; Sharp[4]). Knudsen (1977) gave some evidence that tuna caught in areas where porpoise fishing predominates were generally older and larger than in traditional schoolfish areas. Size overlap, however, did occur (Calkins 1965). Assuming that the number of porpoise schools have declined, the probability of tuna encountering porpoise schools has decreased. The probability of tuna aggregated near flotsam encountering porpoise schools has also decreased. Thus, as a result of decreased encounter rates with porpoise (slower transition from flotsam to porpoise), the size of the aggregations of tuna near flotsam have increased.

In conclusion, the most likely sources of flotsam are the large rivers of Central America. Indirect evidence indicates that tuna caught in unassociated schoolfish sets are from the same population as tuna caught associated with flotsam. It appears that the increase of flotsam-associated sets from 1963 to 1975 was due to an increased interest by fishermen and hence an increased fishing effort on floating objects. The observed increase in catch per set may have been a biological change rather than a change in fishing technology or skill.

ACKNOWLEDGMENTS

I would like to express my thanks to John Hunter who provided guidance in several phases of this study. His comments were extremely help-

[3]Southwest Fisheries Center. 1976. Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Tropical Pacific Yellowfin Tuna Fishery. SWFC Adm. Rep. LJ-76-29, 54 p. Southwest Fisheries Center, La Jolla, CA 92038.

[4]G. Sharp, Inter-American Tropical Tuna Commission, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1977.

ful. Richard McNeely first suggested the possible interaction of porpoise and flotsam-associated tuna. The Inter-American Tropical Tuna Commission provided much of the data. William Flerx and Richard Charter provided insight into the operation of the fishery. Gary Sharp provided useful information about yellowfin tuna. Rainfall data were obtained from Eric Forsbergh. William Lenarz, Douglas Chapman, and Robin Allen reviewed the paper and offered constructive comments.

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DESCRIPTION OF LARVAE OF THE NORTHERN SHRIMP, *PANDALUS BOREALIS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

EVAN HAYNES[1]

ABSTRACT

Northern shrimp, *Pandalus borealis*, were reared in situ in Kachemak Bay, Alaska, from Stage I (first zoeal) through Stage VIII (second juvenile). Each of the six larval stages and first juvenile stage is described and illustrated, and a brief description is given for the second juvenile stage. Apparently larvae of *P. borealis* in Alaska waters have at least one less stage than larvae of *P. borealis* in either British Columbia, Greenland, or Japan waters. Of the known larvae of the North Pacific Ocean, larvae of *P. borealis* are most similar morphologically to larvae of *P. goniurus* but are separable from them by being slightly larger in size and, in zoeal Stages I-III, by bearing more setae on certain appendages, particularly the antennal scale and certain mouth parts. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, the second pereopods are more developed, and the pleopods are fringed with more setae than for larvae of *P. goniurus*. The criterion of the lack of an outer seta on the maxillule for distinguishing zoeae of *Pandalus* from certain other Caridea is shown to be invalid.

In 1972 the National Marine Fisheries Service began studies on the early life history of pandalid shrimp in Alaska waters with the initial objective of describing in detail laboratory-reared larvae of each pandalid species previously unverified. Two previous reports have described larvae of *Pandalus hypsinotus* Brandt reared in the laboratory (Haynes 1976) and *P. goniurus* Stimpson reared in situ in Kachemak Bay, Alaska (Haynes 1978). This report describes and illustrates each of the six larval stages and the first juvenile stage of northern shrimp, *P. borealis* Krøyer, and compares the stages obtained from rearing in situ with descriptions of pandalid shrimp larvae given by other authors. A brief description of the second juvenile stage is included.

MATERIALS AND METHODS

Rearing techniques were identical in all respects to those described in an earlier report on *P. goniurus* (Haynes 1978). Briefly, the technique consists of obtaining Stage I larvae of known parentage in the laboratory, then rearing the larvae in flasks submerged at sea. Larvae from plankton were also reared in flasks at sea in an identical manner beginning with Stage I. Larvae reared in flasks were compared with larvae from plankton for verification of sequence of stage and larval morphology.

Because the paired appendages of the larvae are symmetrical, only one member (the left) is figured. An exception is the mandibles which are drawn in pairs. Orientation of surface of appendages in the figures is given in the figure legends. The figures of the appendages are in part schematic and represent typical setal counts. Variability in setation or segmentation of paired appendages, such as the difference in number of carpal joints between the left and right second pereopods in the megalopa, is mentioned in the text. Carapace length refers to the straight-line distance from posterior margin of orbit to middorsal posterior margin of carapace. Total body length refers to the distance from tip of rostrum to posterior margin of telson, not including telson spines. Terminology, methods of measuring, techniques of illustration, and nomenclature of gills and appendages follow Haynes (1976). Comparison of larvae from plankton with cast skins from flasks was facilitated by first clearing the larvae in 10% KOH. For clarity, setules on setae are usually omitted but spinulose setae are shown.

STAGE I ZOEA

Mean total length of Stage I (Figure 1A) 6.7 mm (range 6.5-7.3 mm; 25 specimens). Live specimens characterized by orange color; conspicuous chromatophores throughout cephalothorax re-

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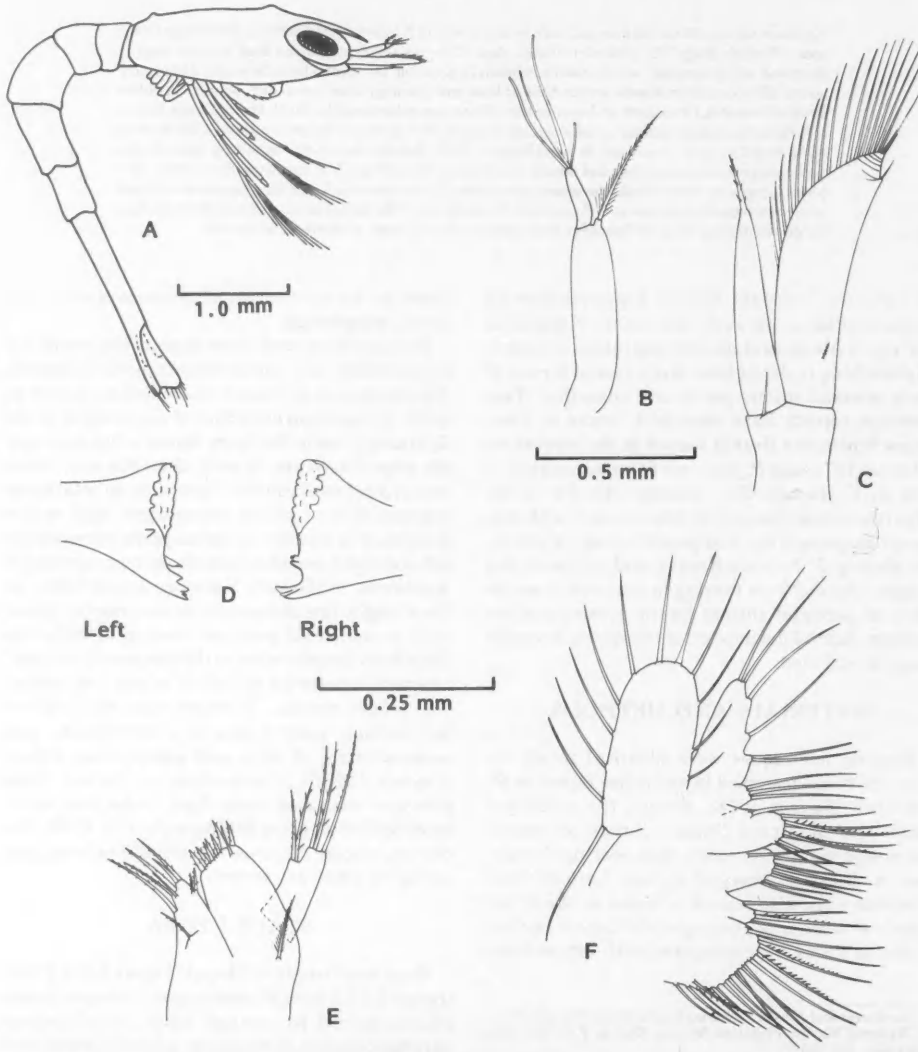
gion, especially in mouth parts; large chromatophore near tip of antennal scale, at base of telson, and at front of eye; smaller but distinct chromatophores on maxillipeds; ventral surface of each abdominal somite tinged orange; faint greenish hue at base of pereopods. Rostrum slender, spiniform, without teeth, about one-third length of carapace, projecting horizontally or slightly downward. Carapace with small, somewhat angular dorsal prominence at base of rostrum and smaller, rounded prominence near posterior edge. These two prominences occur in all zoeal stages. Pterygostomian spines present but usually hidden by sessile eyes. Three or four mi-



nute spinules along ventral margin of carapace immediately posterior to pterygostomian spine (spinules not shown in Figure 1A). These spinules usually occur in all zoeal stages but may vary in number from two to five not only between stages but among individuals within a given stage.

ANTENNULE (Figure 1B).—First antenna, or antennule, consists of simple unsegmented tubular basal portion with heavily plumose seta terminally and distal conical projection with four aesthetascs: one long, one short, and two of intermediate length.

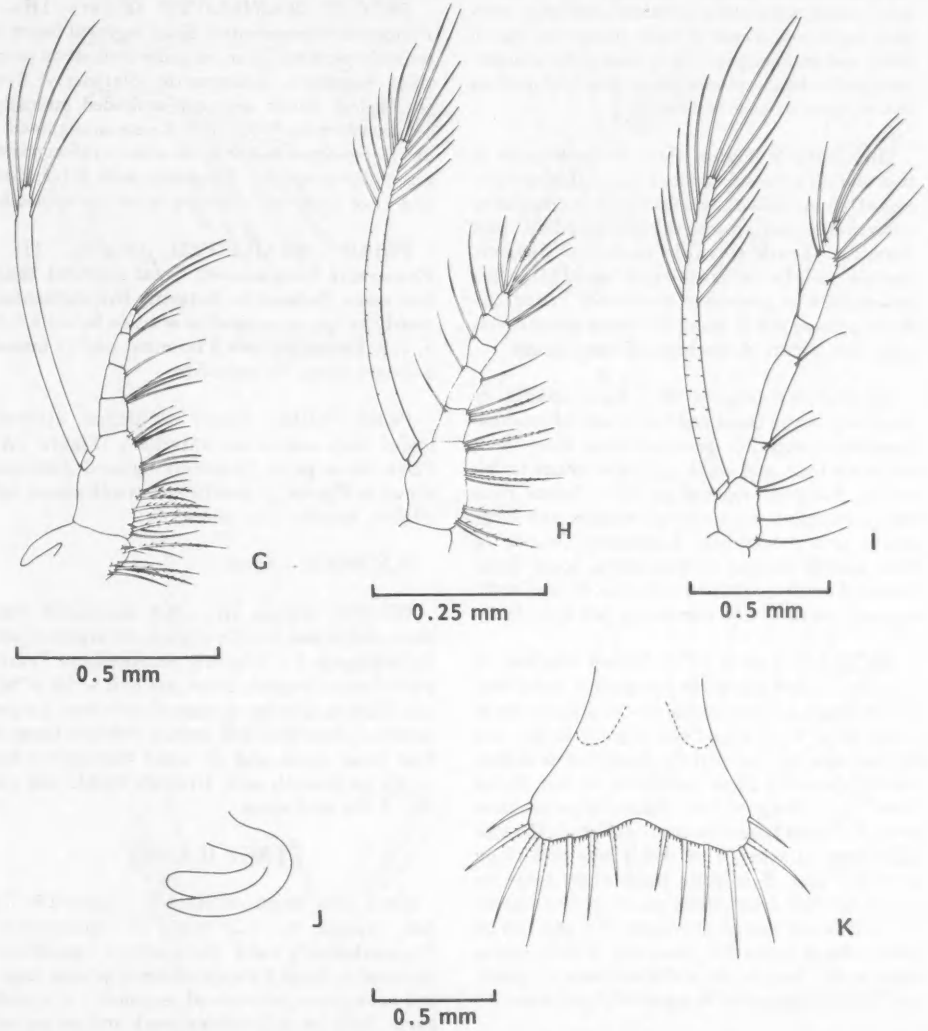


FIGURE 1.—Stage I zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, second pereopod, lateral; K, telson, dorsal.

ANTENNA (Figure 1C).—Second antenna, or antenna, consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, and tipped by spinulose spine. Antennal scale distally divided into six joints (the two proximal joints incomplete) and fringed with 19 heavily plumose setae along terminal and inner margins; small seta occurs on outer margin at base of joints and another proximally near outer margin. Protopodite bears spinous seta at base of flagellum but no spine at base of scale.

MANDIBLES (Figure 1D).—Without palps in this and all succeeding zoeal stages. Incisor process of left mandible bears four teeth in contrast to triserrate incisor process of right mandible. Left mandible bears movable premolar denticle (lacinia mobilis) whereas right mandible bears two immobile premolar denticles. Truncated molar process of left mandible bears subterminal tooth that occurs throughout all zoeal stages.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and endopodite. Coxopodite (proximal lobe) bears stout seta near base, and eight spinulose spines terminally. Basipodite (median lobe) bears nine spinulose spines on terminal margin and large setose seta proximally. Endopodite originates from lateral margin of basipodite; bears three terminal and two subterminal setae, three of them sparsely plumose and remaining two spinulose.

MAXILLA (Figure 1F).—Second maxilla, or maxilla, bears platelike exopodite (scaphognathite) with 11 long, evenly spaced plumose setae along outer margin and one slightly longer and thicker seta at the slightly expanded proximal end. Endopodite gives indication of four partly fused segments and bears nine large plumose setae. Coxopodite and basipodite bilobed. Coxopodite bears 21 setae, 4 on distal lobe and 17 on proximal lobe. Basipodite bears eight setae on each lobe. Five setae, three on coxopodite (one on distal lobe and two on proximal lobe) and two on distal lobe of basipodite, bear row of little spines along entire length. An additional seta on proximal lobe of coxopodite is especially spinulose.

FIRST MAXILLIPED (Figure 1G).—Most heavily setose of natatory appendages. Protopodite fully segmented; bears 7 setae on proximal segment and 18 slightly smaller setae on distal segment, 9 of them spinulose. Endopodite distinctly four-segmented; setation formula 4, 2, 1, 4. Exopodite a longer slender ramus segmented at base; bears two terminal and three or four lateral natatory setae. Epipodite a single lobe.

SECOND MAXILLIPED (Figure 1H).—Protopodite bisegmented; distal segment bears 10 sparsely plumose setae, no setae evident on proximal segment. Endopodite distinctly five-segmented, fourth segment expanded laterally; setation formula 7, 3, 1, 2, 4. A seta on segments 1 and 5 of endopodite and three setae on protopodite especially spinulose. Exopodite with 2 terminal and 11 or 12 lateral natatory setae. No epipodite.

THIRD MAXILLIPED (Figure 1I).—Protopodite bisegmented; distal segment bears four setae. Endopodite distinctly five-segmented; nearly as long as exopodite; setation formula 4, 5, 1, 1, 2. Exopodite with 2 terminal and 14 lateral natatory setae. No epipodite.

PEREOPODS.—Poorly developed, directed under body somewhat anteriorly (Figure 1A). First three pairs biramous (second pereopod shown in Figure 1J), last two pairs uniramous and slightly smaller than pairs 1-3.

PLEOPODS.—Absent.

TELSON (Figure 1K).—Not segmented from sixth abdominal somite; slightly emarginate posteriorly; bears 7 + 7 densely plumose setae. Fourth pair of setae longest, about one-half width of telson. Minute spinules at base of each seta. Larger spinules along terminal margin between bases of four inner pairs and on setae themselves but rarely on seventh pair. Uropods visible and enclosed. No anal spine.

STAGE II ZOEA

Mean total length of Stage II (Figure 2A) 7.5 mm (range 6.7-8.2 mm; 25 specimens). Chromatophore color and pattern essentially identical to Stage I, except chromatophores larger and color more pronounced, especially in mouth parts. Rostrum still without teeth and not curved downward as sometimes in Stage I. Carapace with prominent supraorbital spine and clearly visible antennal and pterygostomian spines. These three

spines persist through all remaining zoeal stages. Epipodite of first maxilliped slightly larger than in Stage I but still not bilobed; pleurobranchiae present as primordial buds.

ANTENNULE (Figure 2B).—Three-segmented; bears large outer and smaller inner flagellum on terminal margin. Flagella not segmented. Inner flagellum conical, bears one long spine terminally. Outer flagellum bears two groups of aesthetascs: one group terminally consisting of eight aesthetascs, two of them larger than remaining six, and a pair of aesthetascs on inner margin. A small budlike projection (not shown in Figure 2B)

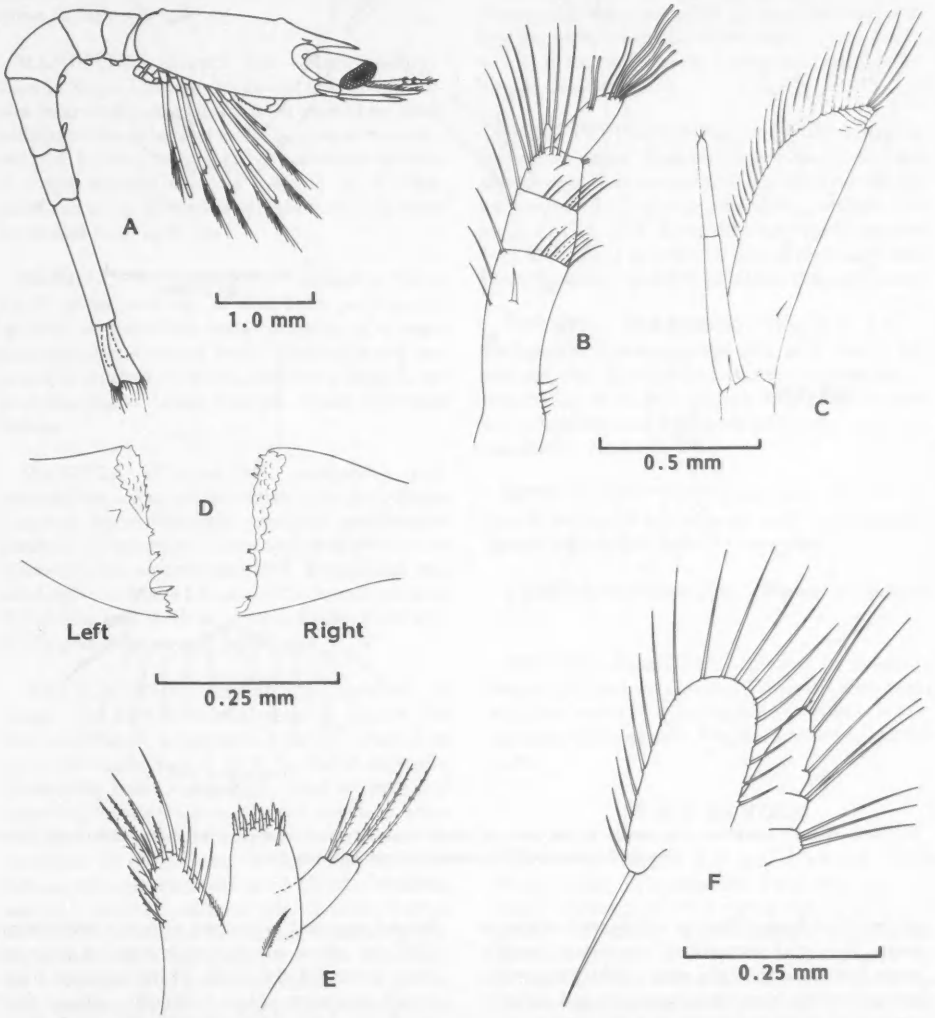


FIGURE 2.—Stage II zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla (exopodite and endopodite), dorsal.

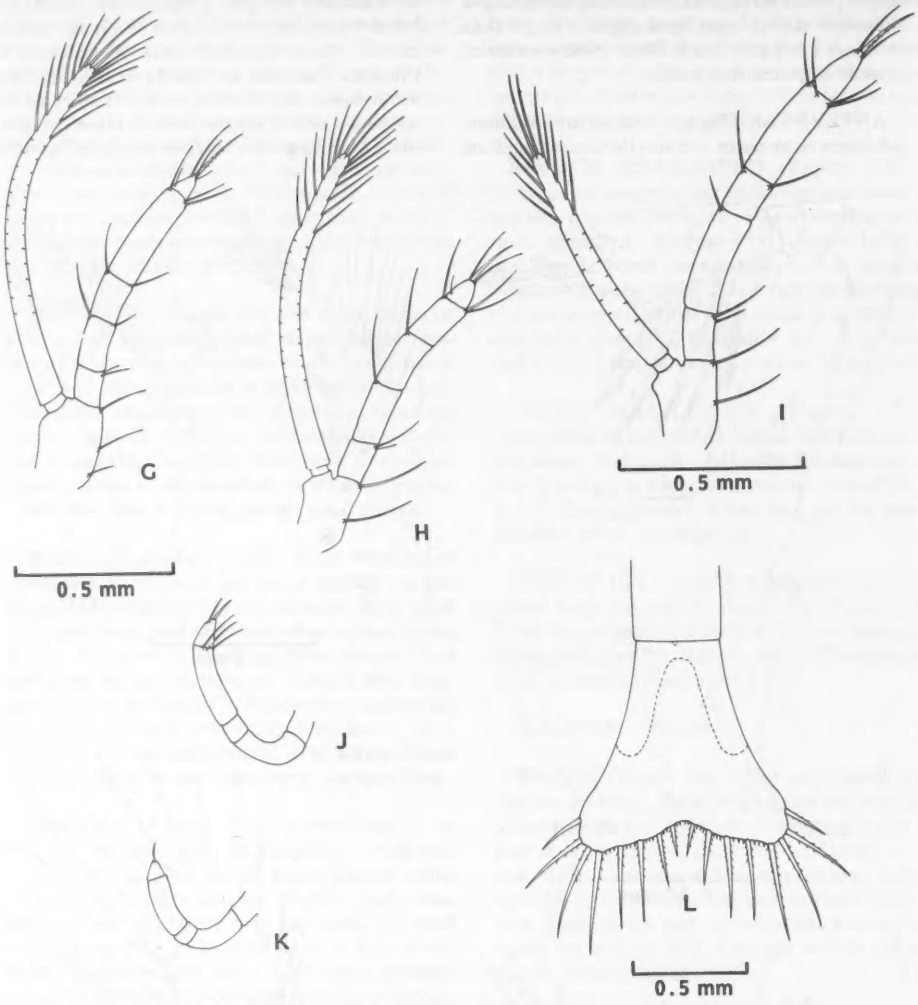


FIGURE 2.—Stage II zoea of *Pandalus borealis*: G, first pereopod, lateral; H, second pereopod, lateral; I, third pereopod, lateral; J, fourth pereopod, lateral; K, fifth pereopod, lateral; L, telson, dorsal.

originates at base of flagella and bears five simple setae. Proximal segment of antennule usually bears five setae laterally near slightly expanded base, three plumose setae laterally and distally, about nine dorsally curving but smaller plumose setae around distal joint, and large spine projecting slightly downward from ventral surface. Second segment bears two plumose setae laterally and about six dorsally curving plumose setae around distal joint. Third segment bears seven plumose setae laterally, about four of them originating ventrally, and three simple setae laterally at base of outer flagellum.

ANTENNA (Figure 2C).—Flagellum two-segmented, still shorter than scale, styliform, and tipped by two small simple setae and short spine. Antennal scale fringed with 25 or 26 long, thin, plumose setae along terminal and inner margins; still has six joints distally but only the three most distal joints complete. Protopodite bears minute spine at base of scale in addition to conspicuous spine at base of flagellum.

MANDIBLES (Figure 2D).—More massive than in Stage I. Incisor processes of both mandibles bear additional tooth. Both mandibles bear additional denticles and molar processes more developed. Lacinia mobilis of left mandible consists of single spinous denticle. Curved lip of truncated end of molar process of right mandible more developed than in Stage I.

MAXILLULE (Figure 2E).—Coxopodite bears 12-15 spines and row of fine hairs proximally; spinules on two of the terminal spines of coxopodite resemble a row of teeth. Basipodite and endopodite essentially unchanged from Stage I, except basipodite bears two additional spinulose spines.

MAXILLA (Figure 2F, exopodite and endopodite).—Exopodite similar in shape to Stage I except more distinctly expanded proximally; bears 17-19 marginal plumose setae in addition to plumose seta at proximal end. Endopodite unchanged from Stage I. Coxopodite bears 3 setae on distal lobe and 17-19 on proximal lobe. Each lobe of basipodite bears additional seta.

MAXILLIPEDS.—Essentially identical to Stage I but bear additional setae as follows. On first maxilliped, protopodite bears 8-10 setae on proximal segment and 19-21 on distal segment; endopodite bears 4, rarely 5, setae on proximal segment; exopodite bears 7 or 8 natatory setae rather than 5 or 6 as in Stage I; no change in epipodite. On second maxilliped, protopodite bears seta on proximal segment and 8-10 setae on distal segment; exopodite bears 14 lateral natatory setae in addition to the 2 terminal setae. On third maxilliped, endopodite bears additional seta terminally on dactylopodite, 2 additional setae on propodite, and additional seta on carpopodite, setation formula 5, 7, 3, 1, 2; exopodite bears 16 lateral natatory setae in addition to 2 terminal setae. No gill buds on second or third maxillipeds.

FIRST PEREOPOD (Figure 2G).—Protopodite bears three setae. Endopodite functionally developed; five-segmented, terminating in simple conical dactylopodite; setation formula 5, 3, 2, 2, 2. Exopodite, longest among pereopods, bears 2 terminal and 14 lateral natatory setae.

SECOND PEREOPOD (Figure 2H).—Protopodite bears two setae. Endopodite similar to first pereopod except shorter; setation formula 4, 3, 1, 1, 2. Exopodite bears 2 terminal and 13 or 14 lateral natatory setae.

THIRD PEREOPOD (Figure 2I).—Protopodite bears two setae. Endopodite one-fourth to one-third longer than exopodite; dactylopodite slightly longer than in first two pereopods; setation formula 3, 4, 2, 1, 2. Exopodite noticeably shorter than exopodites of first and second pereopods and bears 2 terminal and 9 or 10 lateral natatory setae.

FOURTH PEREOPOD (Figure 2J).—Endopodite five-segmented but still poorly developed and directed under body somewhat anteriorly as in Stage I (Figure 2A); dactylopodite and propodite bear two setae and three setae, respectively. No exopodite.

FIFTH PEREOPOD (Figure 2K).—Similar to fourth pereopod but shorter and dactylopodite tipped with single seta. No exopodite.

PLEOPODS (Figure 2A).—Present as distinct buds.

TELSON (Figure 2L).—Similar in shape to Stage I but distinctly jointed from sixth abdominal somite; bears 8 + 8 densely plumose setae. Uropods still enclosed. Anal spine present but minute.

STAGE III ZOEA

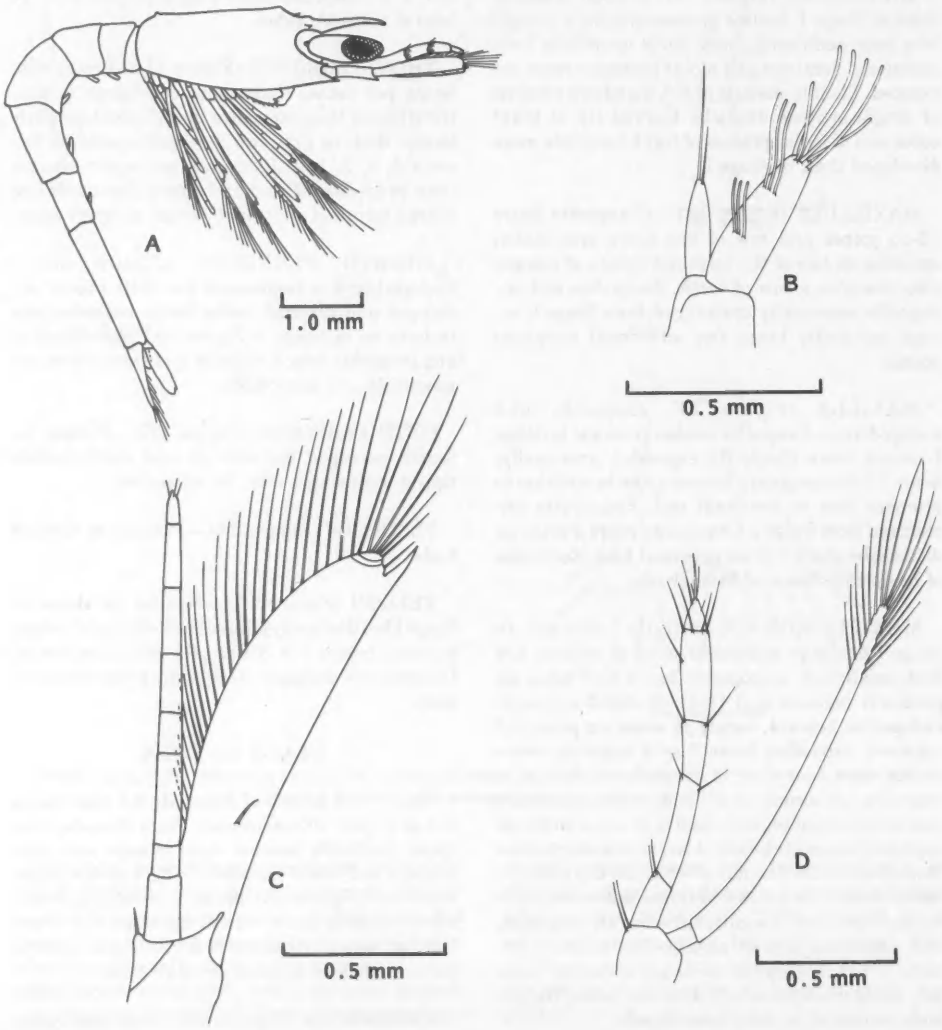
Mean total length of Stage III 9.5 mm (range 9.0-10.0 mm; 10 specimens). From this stage on, zoeae gradually become more orange and color pattern not useful in identifying a given stage. Rostrum (Figure 3A) projects horizontally but curves slightly downward at tip; bears one or two teeth at base. Epipodite of first maxilliped bilobed; pleurobranchiae present as small buds.

ANTENNULE (Figure 3B, inner and outer

flagella).—Flagella not segmented. Inner flagellum about one-half length of outer flagellum, bearing stiff seta at base of terminal spine. Outer flagellum bears four long and two shorter aesthetascs terminally and two groups of three aesthetascs each proximally.

ANTENNA (Figure 3C).—Flagellum eight-segmented, about equal in length to scale, tipped by three short setae and remnant of terminal spine. Antennal scale narrower than in Stage II and fringed with about 30 plumose setae; two complete joints at tip. Spine on protopodite at base of scale considerably larger than in Stage II.

MAXILLIPEDS.—Change in form and setation of maxillipeds from Stage III on is slight and consists primarily of second maxilliped becoming



curved as in adult and its propodite slightly widened, third maxilliped becoming shaped as in adult, and natatory setae on exopodites of second and third maxillipeds increasing in number to usually 20 in Stage V.

FIRST PEREOPOD (Figure 3D).—Has begun to acquire adult shape, particularly in widened propodite and carpopodite segments.

SECOND PEREOPOD (Figure 3E).—Similar to Stage II except distal joint of propodite projects slightly anteriorly.

THIRD, FOURTH (Figure 3F), AND FIFTH PEREOPODS.—Endopodites similar; like first pereopod have begun to acquire adult shape, especially in lengthened dactylopodite and widened propodite. Ischiopodite articulates somewhat laterally with meropodite.

PLEOPODS (Figure 3G, second pleopod).—Bilobed, unsegmented, and without setae.

TELSON (Figure 3H).—Endopodite not fully developed; about one-third length of exopodite and bearing several setae along lateral and posterior margins. Uropods free. Anal spine clearly visible.

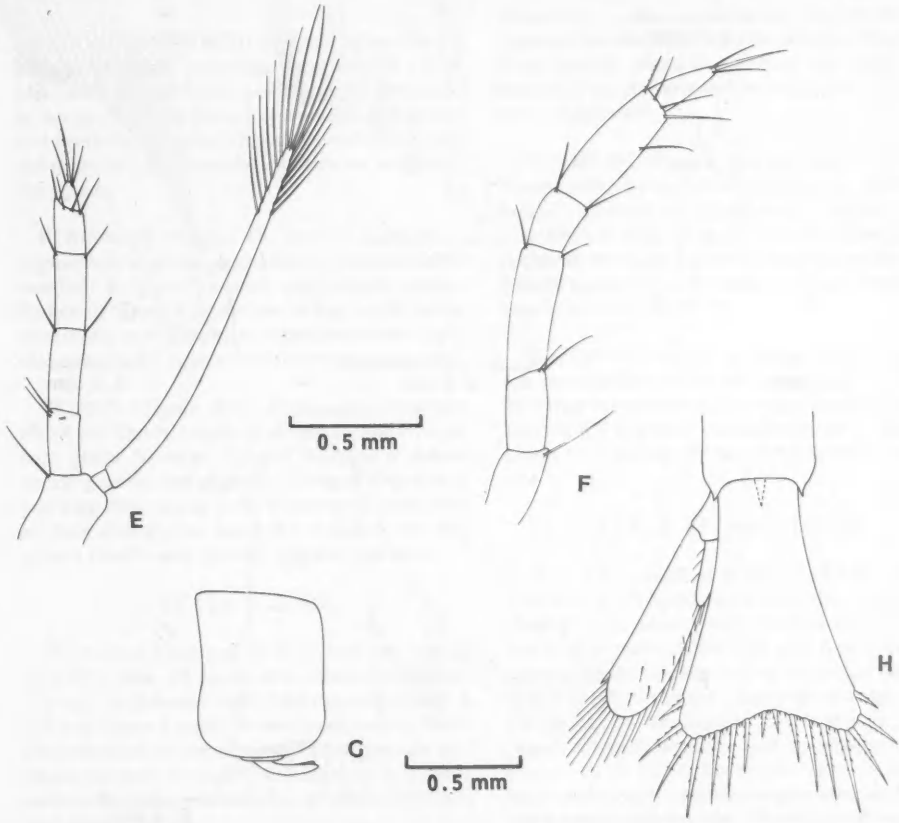


FIGURE 3.—Stage III zoea of *Pandalus borealis*: A, whole animal, right side; B, antennule (inner and outer flagella), ventral; C, antenna, ventral; D, first pereopod, lateral; E, second pereopod, lateral; F, fourth pereopod, lateral; G, second abdominal somite and pleopod, right side; H, telson, dorsal.

STAGE IV ZOEA

Mean total length of Stage IV 13.0 mm (range 12.6-13.2 mm; 10 specimens). Rostrum (Figure 4A) bears four to eight but usually six teeth dorsally, no teeth ventrally; tip not bifid. No change in epipodite of first maxilliped or pleurobranchiae except slight increase in size. Epipodite on second maxilliped present as small bud. No mastigobranchiae.

ANTENNULE (Figure 4B, inner and outer

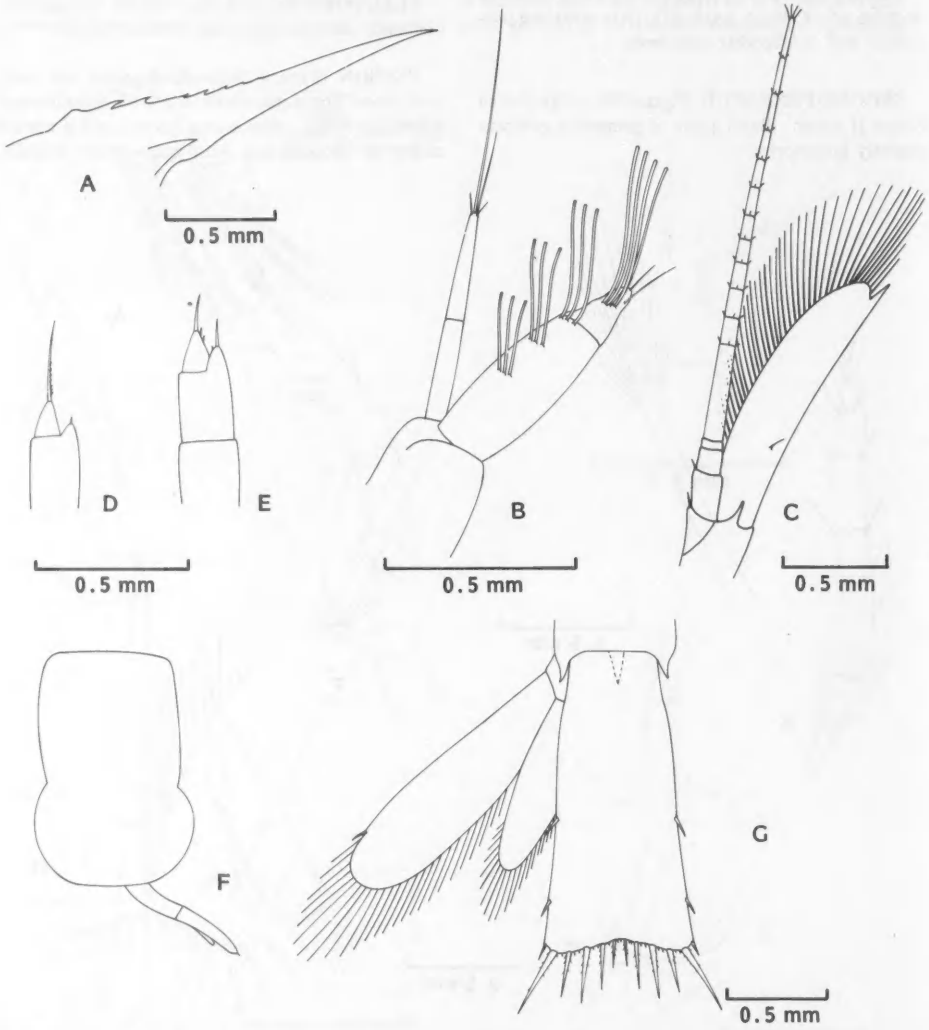


FIGURE 4.—Stage IV zoea of *Pandalus borealis*: A, rostrum, right side; B, antennule (inner and outer flagella), ventral; C, antenna, ventral; D, first pereopod (distal segments only), lateral; E, second pereopod (distal segments only), lateral; F, second abdominal somite and pleopod, right side; G, telson, dorsal.

flagella).—Flagella two-segmented. Inner flagellum nearly as long as outer flagellum. Outer flagellum bears four aesthetascs and two spines terminally and three groups of three aesthetascs each on proximal segment.

ANTENNA (Figure 4C).—Flagellum 15-segmented; 1.5-2 times length of scale, extending past tips of plumose setae fringing antennal scale. Antennal scale without joints at tip. Other than increase in size, changes in antennal scale from Stage IV onward are negligible.

FIRST PEREOPOD (Figure 4D).—Distal joint of propodite projected anteriorly and tipped with small spine.

SECOND PEREOPOD (Figure 4E).—Distal joint of propodite projected anteriorly to about one-half length of dactylopodite; projection tipped by two spines, one terminal and other subterminal and much shorter. Dactylopodite bears one terminal spine and two considerably shorter subterminal spines.

PLEOPODS (Figure 4F, second pleopod).—Segmented; length of second pair of pleopods about one-half height of second abdominal somite. Exopodite usually bears one to four small setae terminally and endopodite sometimes bears single seta terminally. Appendices internae not present.

TELSON (Figure 4G).—Endopodite of uropod about two-thirds length of exopodite and fringed with about 20 setae. Lateral margins of telson nearly parallel but slightly divergent posteriorly and bear two spines each. Posterior margin still slightly emarginate; bears 6 + 6 spines, the outermost (sixth) pair usually without spinules.

STAGE V ZOEA

Mean total length of Stage V 16.0 mm (range 15.2-17.1 mm; 10 specimens). Rostrum (Figure 5A) with 9-12 dorsal teeth, bifid tip, and usually 4, but sometimes 5, partially developed ventral teeth. Pleurobranchiae curve somewhat anteriorly and edges minutely lobulate. Mastigobranchiae occur as minute buds on protopodite of third maxilliped and pereopods 1-4.

ANTENNULE (Figure 5B, flagella only).—Inner flagellum four-segmented. Outer flagellum four- or five-segmented; bears six groups of three aesthetascs each. Each segment bears at least one seta but number and location of setae somewhat variable.

ANTENNA (Figure 5C).—Flagellum 2-3 times length of scale.

FIRST PEREOPOD (Figure 5D, distal segments only).—Projection of propodite at least one-half length of dactylopodite; bears two small spines, one terminally and one subterminally. Dactylopodite bears small spine subterminally in addition to terminal spine.

SECOND PEREOPOD (Figure 5E, distal segments only).—Chela well formed. Terminal spine of propodite shorter and stouter than in Stage IV. Dactylopodite bears five spines, the distal two especially stout. Carpopodite usually at least partially segmented.

PLEOPODS (Figure 5F, second pleopod).—Second pair of pleopods about equal in length to height of second abdominal somite; outer flagellum fringed with 11 or 12 plumose setae, inner flagellum with about 8 setae. Appendices internae usually present on pleopods 2-5; tips sometimes bear a few cincinnuli.

TELSON (Figure 5G).—Lateral margins of telson essentially parallel and bear two spines each. Posterior margin straight or slightly emarginate, bearing 6 + 6 spines. Uropods similar in shape to adult; no evidence of transverse hinge of exopodite.

STAGE VI (MEGALOPA)

Mean total length of Stage VI 18.5 mm (range 17.4-20.2 mm, 5 specimens). Rostrum (Figure 6A) shaped as in adult; bears 13-15 dorsal teeth in addition to distinct bifid tip, and 6 or 7 distinct ventral teeth. Usually one or two setae between dorsal teeth. Carapace lacks supraorbital spine. Exopodites on maxillipeds and pereopods 1-3 reduced. Pleurobranchiae and mastigobranchiae shaped as in adult. Inner and outer flagella of antennule eight- to nine-segmented and five-segmented, respectively. Flagellum of antenna about 6 times length of antennal scale. Mandibles still without palps. Chaelae of first and second pereopods shaped as in adult; carpal joints of left

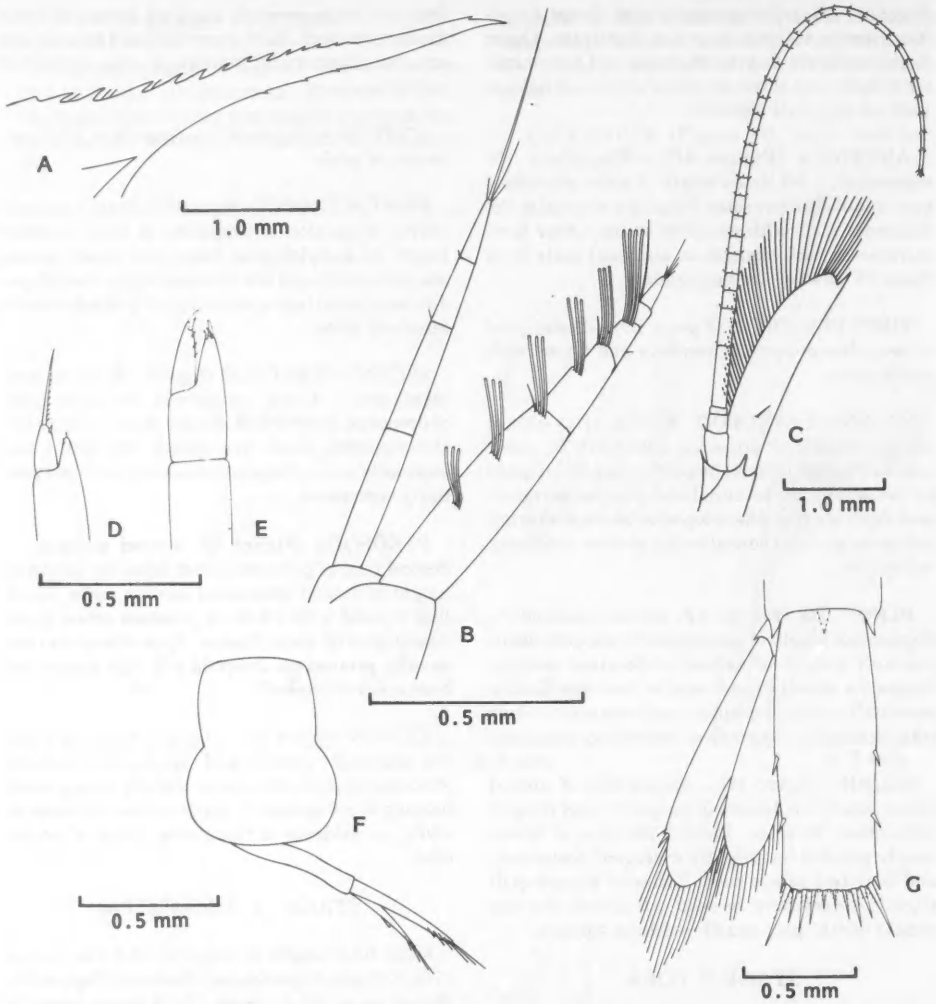


FIGURE 5.—Stage V zoea of *Pandalus borealis*: A, rostrum, right side; B, antennule (flagella only), ventral; C, antenna, ventral; D, first pereopod (distal segments only), dorsal; E, second pereopod (distal segments only), dorsal; F, second abdominal somite and pleopod, right side; G, telson, dorsal.

and right second pereopods 20-25 and 10-13, respectively. Pleopodal setae extend along entire lateral margins of both flagella; tips of appendices internae bear several distinct cincinnuli. Length of second pair of pereopods, excluding setae, 1.5-2 times height of second abdominal segment. Telson (Figure 6B) shows, for first time, shape and spination similar to adult; lateral margins converge posteriorly but widen slightly at junction with posterior margin; typically four spines on each lateral margin but in this stage and Stages VII and VIII one lateral spine often lacking. Posterior margin of telson rounded but not as much as in Stage VII; bears 3 + 3 stout spines and sometimes

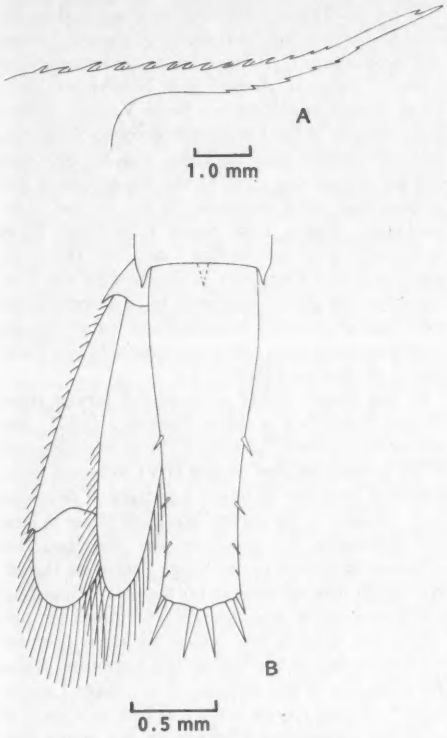


FIGURE 6.—Stage VI (megalopa) of *Pandalus borealis*: A, rostrum, right side; B, telson, dorsal.

remnants of a spine or two from Stage V. Transverse hinge of exopodite of uropod complete.

STAGES VII AND VIII (JUVENILES)

Mean total length of Stage VII (first juvenile) 18.4 mm (range 15.1-21.0 mm; 5 specimens). Usually two setae between most rostral teeth. Carapace without supraorbital spine. Arthrobranchiae on third maxilliped and pereopods 1-4 present as minute buds. Mandibular palp present for first time; three-segmented. Inner and outer flagella of antennule each 11- to 13-segmented. Exopodites on maxillipeds and pereopods 1-3 remnant. Third abdominal somite sometimes bears minute spine on middorsal posterior margin. Carpal joints of left and right second pereopods 28-30 and 14-17, respectively. Lateral margins of telson (Figure 7) typically bear 5 + 5 spines; posterior margin rounded as in adult.

Mean total length of Stage VIII (second juvenile) 21.6 mm (range 19.0-23.6 mm; 8 specimens). Morphological differences between Stages VII and VIII slight. Most notable features of Stage VIII: at least three or four setae between most rostral spines; complete lack of exopodites on third maxilliped and pereopods 1-3; inner and outer flagella of antennule each 15- to 16-segmented; lateral margins of telson typically bear 6 + 6 spines.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

The first description of larvae ascribed to *Pandalus borealis* was given by Sars (1900), based on specimens collected from plankton. Berkeley (1931) showed that Sars' larvae could not be *P. borealis*; almost simultaneously Lebour (1930) showed that they were *Caridion gordoni* (Bate). Sars' "post-larval" specimen, however, is considered by both Lebour and Berkeley to be correctly identified as *P. borealis*. As far as can be compared, my Stage VI (megalopa) and Sars' "post-larval" specimen are essentially identical except for the

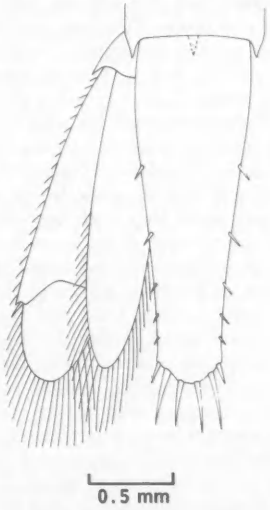


FIGURE 7.—Stage VII (first juvenile) of *Pandalus borealis*: telson, dorsal.

rostral tip, which in my larva is bifid but in Sars' is styliform, and the chela of the first pereopod, which is completely developed in my larva but not in Sars'.

Stephensen (1912) described zoeal Stages I to V from plankton that he provisionally identified as "*P. propinquus* (?)" and Stage III zoeae (1916) as "*Spirontocaris*-larva No. 4." Berkeley (1931) noted the close similarity of the "*P. propinquus* (?)" specimens to zoeae of *P. borealis* from British Columbia waters. Stephensen (1935) later decided that both "*P. propinquus* (?)" and "*Spirontocaris*-larva No. 4" were actually zoeae of *P. borealis*. He also compared his zoeae with fragments of a specimen identified by Krøyer as *Dymas typus* and decided Krøyer's specimen was a Stage IV zoea of *P. borealis*.

Comparing the description and figures of Stephensen's (1912) zoeae and mine in general for each stage, my zoeae are slightly more advanced than Stephensen's. In my Stage I zoeae the antennal scale bears 19 plumose setae; the basipodite and coxopodite of the maxillule bear 9 + 1 and 9 spines, respectively; the endopodite of the first maxilliped is segmented; and the exopodites of maxillipeds 1, 2, and 3 bear 6, 14, and 16 natatory setae, respectively. In Stephensen's Stage I zoeae the antennal scale bears only eight or nine plumose setae; the basipodite and coxopodite of the maxillule bear five and six spines, respectively; the endopodite of the first maxilliped is not segmented; and the exopodites of maxillipeds 1, 2, and 3 bear 4, 10, and 10 natatory setae, respectively. In Stage II, the relative difference in number of setae and spines between my zoeae and Stephensen's remains essentially the same, except in my zoeae the exopodites of pereopods 1, 2, and 3 bear 16, 16, and 12 setae, respectively, whereas in Stephensen's zoeae they each bear 18 setae. In Stage III, the rostrum of my zoeae bears only a single tooth and the antennal flagellum is eight-jointed, but in Stephensen's zoeae the rostrum bears as many as three teeth and the antennal flagellum is not jointed. In Stage IV, the rostrum of my zoeae bears six or seven teeth, the antennal flagellum is 15-segmented, and the telson bears eight pairs of spines whereas in Stephensen's zoeae the rostrum bears only four teeth, the antennal flagellum is still unsegmented, and the telson bears only seven pairs of spines. In Stage V, the most obvious difference is that the pleopods are segmented in my zoeae but not in Stephensen's.

In his 1916 report, Stephensen described an additional larva which he considered the sixth stage of *P. propinquus* G. O. Sars; later (1935) he decided it was *P. borealis*. According to Stephensen, this stage closely resembles his Stage V zoeae, differing primarily in the left second pereopod being considerably longer than the right, and, for both second pereopods, the joint at the distal end of the carpopodite being complete. In my larvae, morphological change from Stage V to Stage VI is sufficiently pronounced that I consider the sixth stage to be the megalopa. If Stephensen was correct in assuming his specimen to be a sixth stage zoea, then *P. borealis* in Greenland waters has at least six zoeal stages compared with only five zoeal stages in Alaska waters.

In her classic study of pandalid larvae from British Columbia waters, Berkeley (1931) described and figured *P. borealis* Stage I zoeae reared in the laboratory and Stages II-VI collected from plankton. Her larvae follow a pattern of development similar to my larvae but each stage is less well developed. For instance, she described the antennal flagellum in her Stage I zoeae as tipped by a simple seta whereas in my zoeae it is tipped by a spinulose spine, and she neither figured nor described the spinous seta which my zoeae bear on the protopodite at the base of the flagellum. Also, the exopodite of the maxilla of her Stage I zoeae bears 8-10 long simple setae and has no trace of a proximal expansion whereas in my zoeae the exopodite of the maxilla bears 11 long plumose setae as well as one longer, thicker seta at the proximal end which is slightly expanded. In Stage II, the outer flagellum of the antennule of Berkeley's zoeae is figured as bearing only three aesthetascs distally whereas my zoeae bear eight. The proximal expansion of the exopodite of the maxilla is "just appearing" in Berkeley's Stage II but in mine it is distinctly expanded. Moreover, she described the telson as being still indistinctly segmented from the sixth abdominal somite but in my zoeae it is always distinctly segmented at Stage II. Berkeley's Stage III zoeae are essentially identical to mine as far as can be determined from her description. Her Stage IV zoeae have four small teeth at the base of the rostrum, the pleopods are without joints, and there is no epipodite on the second maxilliped. In my Stage IV zoeae, the rostrum usually has six teeth, the pleopods are jointed, and an epipodite occurs on the second maxilliped. In Stage V, the rostral tip of Berkeley's zoeae is still styliform. There is no evidence

from either her description or figure of ventral teeth on the rostrum, and the pleopods have not yet developed appendices internae. In my Stage V zoeae the rostral tip always bears at least a protuberance indicative of the bifid tooth, and pleopods 2-5 bear at least partially developed appendices internae. In contrast to my Stage VI, the megalopa, Berkeley's Stage VI is still typically zoeal: there is still no mention of ventral rostral teeth, the carapace still bears a supraorbital spine, the carpopodites of the second pereopods are not segmented, and the telson bears three pairs of lateral spines (not including the sixth terminal pair) and terminal setal pairs 2-4 have begun to degenerate.

Berkeley (1931) also mentioned a *P. borealis* larva she obtained from plankton that, according to her, corresponds to the sixth stage of *P. danae* Stimpson and is similar to that described by Sars (1900) as the "post-larval" stage of *P. borealis*. Berkeley's sixth stage and Sars' "post-larval" stage are typically nonzoeal as indicated by the lack of supraorbital spines, segmentation of the carpopodites of the second pereopods, degeneration of the pereopodal and third maxilliped exopodites, and the typically adult shape and spination of the telson. Because this stage would be at least the seventh stage, it appears that *P. borealis* in British Columbia waters, as well as Greenland waters (Stephensen 1916), has at least six zoeal stages compared with only five zoeal stages in Alaska waters.

The preceding comparisons show that Berkeley's zoeae were less well developed at each given stage than mine and an additional stage or two was probably necessary for her zoeae to reach the megalopa stage. An apparent contradiction to this delayed development is the lack of segmentation of the antennal scale in the early stages of Berkeley's zoeae. As shown by Haynes (1976), however, Berkeley was mistaken in this regard and her specimens undoubtedly possessed a segmented scale in the early stages.

The only other description of larvae of *P. borealis* known to me is that of Kurata (1964) who, like Berkeley (1931), obtained Stage I zoeae in the laboratory from known parentage but Stages II-VII from plankton. Kurata's zoeae are essentially identical to mine through Stage V, except the rostrum of Kurata's Stage V zoeae is identical to the rostrum of my Stage IV zoeae. Kurata's Stage VI corresponds to my Stage V, but his Stage VII possesses characteristics intermediate between my Stages V and VI. For instance, in Kurata's Stage VII the exopodites on pereopods 1-3 and the third maxilliped have not begun to degenerate nor are the carpopodites segmented whereas in my Stage VI (megalopa) the exopodites on pereopods 1-3 and the third maxilliped are reduced and the carpopodites of the left and right second pereopods are segmented. Also, the lateral spination and shape of the telson of Kurata's Stage VII are typical of postzoeae but posteriorly the telson bears 6 + 6 spines, a typically zoeal characteristic. By studying Stage VII individuals just prior to molting, Kurata found that Stage VIII individuals possessed a distinct mandibular palp and degeneration of posterior telson spines 2-4. He concluded that Stage VII was the last zoeal stage and Stage VIII the first postzoea, or megalopa.

According to Lebour (1930), the lack of an outer seta on the maxillule in zoeae of *Pandalus* is one criterion for distinguishing this genus from certain other Caridea. Pike and Williamson (1964), however, found the seta consistently present in early stages of British species of *Pandalus*. Occurrence of the seta in Stage I zoeae has been reported by Gurney (1942) for *Pandalus montagui* Leach and *P. stenolepis* Rathbun; by Kurata (1955, 1964) for *P. borealis* and *P. kessleri* Czerniavski; and Modin and Cox (1967) for *P. jordani* Rathbun. I have consistently found the seta in the early stages of *P. hypsinotus*, *P. goniurus*, and *P. borealis*. Lebour's suggestion that the lack of the seta is a distinguishing criterion for zoeae of *Pandalus* should, therefore, be disregarded.

In addition to *P. borealis*, larvae have been described, at least in part, for nine other species of pandalids from the North Pacific Ocean: *P. goniurus, P. jordani, P. platyceros* Brandt, *P. danae, P. kessleri, P. hypsinotus, P. stenolepis, Pandalopsis dispar* Rathbun, and *P. coccinata* Urita. Of these nine species, larvae of *Pandalus stenolepis, P. jordani,* and *P. goniurus* are most like larvae of *P. borealis*, being characterized by exopodites on pereopods 1-3 rather than only on pereopods 1 and 2 and by poorly developed pereopods in Stage I. Zoeae of *P. stenolepis* were described by Needler (1938). Based on her descriptions, zoeae of *P. stenolepis* are readily distinguished from zoeae of *P. borealis* by 1) the shape and spination of the rostrum, which in Stage I *P. stenolepis* is about as long as the carapace and projects upward rather than downward as in *P. borealis*, and 2) the fringed posterior edge of the abdominal somites and the serrated margins of

the carapace, both of which persist to Stage V in *P. stenolepis* but never occur in *P. borealis*.

Larvae of *P. jordani* have been described from specimens reared in the laboratory. Compared with development of similar species, Modin and Cox (1967) and Lee (1969) obtained more stages (11-13 and at least 8, respectively) than expected for larvae of *P. jordani* from plankton. Because of the possibility of these extra stages, only Stage I zoeae of *P. borealis* and *P. jordani* can be compared. Upon hatching, zoeae of *P. borealis* are slightly more developed than zoeae of *P. jordani*. For instance, in Stage I *P. jordani*, the exopodites of maxillipeds 1, 2, and 3 bear 4, 9-11, and 11 or 12 natatory setae, respectively; the left mandible bears no lacinia mobilis; the basipodite of the maxillule bears six spines terminally; and the scaphognathite of the maxilla bears seven to nine setae along its outer margin. In Stage I *P. borealis*, maxillipeds 1, 2, and 3 bear 5 or 6, 13 or 14, and 16 natatory setae, respectively; the left mandible bears a single lacinia mobilis; the basipodite of the maxillule bears 9 spines terminally; and the scaphognathite of the maxilla bears 12 setae along its outer margin. Beyond Stage I, the most distinguishing difference between zoeae of *P. jordani* and *P. borealis* seems to be the development of the rostral tip which in zoeae of *P. jordani* remains acuminate but in zoeae of *P. borealis* becomes bifid in later stages.

In an earlier report (Haynes 1978), I described larvae of *P. goniurus* reared in the same manner as larvae of *P. borealis* described here. Larvae of both species are morphologically similar, especially in early stages, and often occur together in plankton. To facilitate identification of larvae of these two species, the most readily observable morphological differences are listed by stage in Table 1. Larvae of *P. goniurus* are characteristically smaller than those of *P. borealis* and in

TABLE 1.—Morphological characteristics for distinguishing between larvae of *Pandalus borealis* and *P. goniurus* reared in situ in Kachemak Bay, Alaska.

Stage and characteristic	*P. borealis*	*P. goniurus*
Stage I zoea:		
Mean total length (mm)	6.7 (range 6.5-7.3; 25 specimens)	4.0 (range 3.7-4.2; 10 specimens)
No. of plumose setae fringing antennal scale	19	9
No. of spines terminally on basipodite of maxillule	9	5
No. of plumose setae on scaphognathite (in addition to single proximal seta)	11	4
No. of nataory setae on exopodites:		
Maxillipeds 1, 2, 3,	5-6, 13-14, 16	4, 8, 12
Stage II zoea:		
Mean total length (mm)	7.5 (range 6.7-8.2; 25 specimens)	5.9 (range 4.5-5.3; 10 specimens)
No. of plumose setae fringing antennal scale	About 25	About 19
No. of natatory setae on exopodites:		
Maxillipeds 1, 2, 3,	7, 16, 18	6, 12, 14
Pereopods 1, 2, 3,	16, 16, 12	12, 8, 8
Stage III zoea:		
Mean total length (mm)	9.5 (range 9.0-10.0; 10 specimens)	6.2 (range 6.0-6.6; 10 specimens)
Rostrum	1-2 conspicuous teeth	1 inconspicuous tooth
Antennal flagellum	8-segmented	3-segmented
Antennal scale	About 30 setae	About 20 setae
Stage IV zoea:		
Mean total length (mm)	13.0 (range 12.6-13.2; 10 specimens)	7.7 (range 6.8-8.3; 10 specimens)
Rostrum	6-7 dorsal teeth	2 dorsal teeth
Antennal flagellum	About 1½ × scale, extending past tips of plumose setae	Longer than scale but not extending past tips of plumose setae
Propodite of pereopod 2	Projected anteriorly about ½ length of dactylopodite	Projected anteriorly only slightly
Pleopods	Segmented, pleopod 2 about ½ height of abdominal somite	Unsegmented, pleopod 2 about 1/3 height of abdominal somite
Stage V zoea:		
Mean total length (mm)	16.0 (range 15.2-17.1; 10 specimens)	10.3 (range 8.2-11.3; 10 specimens)
Rostrum	9-12 dorsal teeth; tip bifid; 4-5 partially developed ventral teeth	5-6 dorsal teeth; tip not bifid (but may show slight protuberance); no ventral teeth
Chela of pereopod 2	Fully formed	Not fully formed, propodite extension about ½ length of dactylopodite
Pleopods	With appendices internae; fringed with plumose setae; pleopod 2 as long or longer than height of abdominal somite	Without appendices internae; 2-4 simple setae terminally; pleopod 2 about 2/3 height of abdominal somite
Stage VI (megalopa):		
Mean total length (mm)	18.5 (range 17.4-20.2; 5 specimens)	13.8 (range 11.1-15.8; 6 specimens)
Rostrum	13-15 dorsal teeth, 6-7 ventral teeth	8-9 dorsal teeth, 4-5 ventral teeth

Stages I-III the number of setae on certain appendages, particularly the antennal scale and certain mouthparts, is fewer than for zoeae of *P. borealis*. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, the second pereopods are more developed, and the pleopods are fringed with more setae than for larvae of *P. goniurus*.

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RELATIONSHIPS OF THE BLUE SHARK, *PRIONACE GLAUCA*, AND ITS PREY SPECIES NEAR SANTA CATALINA ISLAND, CALIFORNIA[1]

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ABSTRACT

Small fishes and cephalopods associated with both pelagic and inshore habitats composed the major prey for the blue shark, *Prionace glauca*, near Santa Catalina Island, Calif. The northern anchovy, *Engraulis mordax*, was the predominant prey for sharks in the immediate study area while at least 13 species of pelagic cephalopods constituted major prey for sharks in more distant oceanic waters. Inshore species taken by sharks included pipefish, *Syngnathus californiensis*; jack mackerel, *Trachurus symmetricus*; and blacksmith, *Chromis punctipinnis*. In addition, sharks moved inshore to feed on winter spawning schools of market squid, *Loligo opalescens*. Digestive rate studies and telemetric monitoring of activity patterns indicate that sharks forage in waters near the surface from around midnight through dawn. Diel activities of prey species were examined and show that most prey dispersed in the upper water column at night and refuged during the day either by schooling (anchovies and jack mackerel) or by retreating to deeper waters (pelagic cephalopods). Field observations of shark feeding behavior indicate that predatory modes vary in response to prey behavior.

The blue shark, *Prionace glauca* (Carcharhinidae) (Figure 1), is a pelagic carnivore cosmopolitan in tropical and warm temperate seas. Because of its pelagic habits, the majority of ecological studies on this species have been predicated on data from sharks captured by sport and commercial fisheries. As a result data has been largely qualitative, and the shark's role as a predator in the epipelagic habitat has remained unclear.

The importance of small fish as prey items for blue sharks has been described by Couch (1862), Lo Bianco (1909), Bigelow and Schroeder (1948), Strasburg (1958), LeBrasseur (1964), Bane (1968), Stevens (1973), and others. These prey generally are schooling species common in productive coastal waters. Cephalopods were also reported as major prey but little information is available on specific identifications (see Stevens 1973; Clarke and Stevens 1974).

Although blue sharks have been observed feeding on dead or wounded cetaceans (Bigelow and Schroeder 1948; Cousteau and Cousteau 1970) there is little indication that they habitually prey on live, healthy marine mammals. The occurrence of mammalian tissue in the diet of blue sharks is rare (Strasburg 1958; Stevens 1973), and such feeding is most likely directed to dead mammals or those in poor health. Air/sea disasters have resulted in attacks on humans by blue sharks (see Schultz and Malin 1963; Fitch[3]) but these cases usually involved injured persons or corpses.

Standard tagging programs (Weeks 1974; Casey 1976; Stevens 1976) and telemetric trackings (Sciarrotta and Nelson 1977) have provided some information on large-scale movements of blue sharks but relatively little is known of their orientation mechanisms and predatory behavior.

Despite the profusion of descriptive reports, there still exists a great need for quantitative data on ecological relationships between the blue shark and its prey species. With these ideas in mind, I undertook this study within a limited geographic area to 1) provide a quantitative assessment of the diet of blue sharks near Catalina Island, 2) establish temporal and/or geographical shifts in food habits, and 3) describe behavioral interactions between the blue shark and its prey species.

METHODS

The study area was located north of the Isthmus, Santa Catalina Island, Calif. (Figure 2). Beds of

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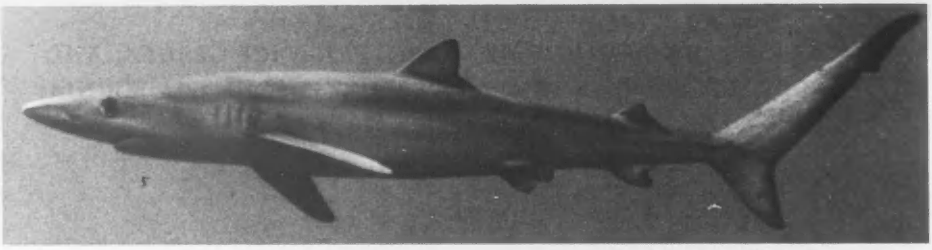

FIGURE 1.—Female blue shark near the ocean surface.

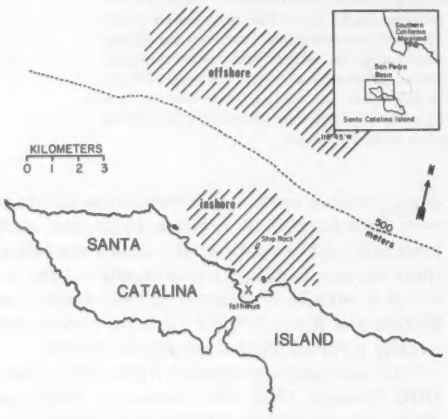

FIGURE 2.—Study area at Catalina Island, Calif. Hatching indicates sampling regions. Sharks feeding among squid schools were observed at ×.

giant kelp, *Macrocystis pyrifera*, composed the major habitat along the island shore. A submarine shelf, averaging 150 m deep, extends approximately 2 km seaward then slopes to depths near 900 m and forms the floor of the San Pedro Basin. "Inshore" sampling stations were located above the shelf within 3 km of the island, and "offshore" stations centered approximately 6 km north of the Isthmus, over deeper basin waters.

Sharks were collected monthly between March 1975 and March 1976. Samples were taken during morning and afternoon hours at both inshore and offshore areas with an attempt to maintain a consistent area-time sampling schedule. Sharks were attracted to a drifting 7-m work boat by baiting with slashed Pacific mackerel, *Scomber japonicus*, suspended in a wire basket 5 m beneath the surface. Once attracted, sharks were captured by hook and hand line using mackerel or market squid, *Loligo opalescens*, as bait. Sharks were landed as quickly as possible to minimize regurgitation and then measured, sexed, and inspected for mating scars and general health. Contents of esophagi and stomachs were filtered through 1-mm mesh netting and preserved. Recognizable prey items and their digestive states were recorded on site. Intestinal tracts were occasionally examined but contributed little information on the diet because of the small pylorus which restricted passage of identifiable prey fragments.

Except for the market squid, cephalopods in the diet were represented exclusively by beaks. Beaks were paired into sets of upper and lower halves, and identified when possible according to Clarke (1962) and Pinkas et al. (1971). Specific identifications were verified by comparisons with beaks from collections of local species. Whole volumes of squid were estimated from beak-size/body-weight regressions for the major cephalopod families given by Clarke (1962). For calculations, the density of cephalopod flesh was assumed to be 1 g/cm^3. A regression for the family Ocythoidae (not given by Clarke) was generated by plotting beak measurements and body weights from local specimens on Clarke's Octopodidae and Argonautidae regressions and constructing a parallel relationship curve. Beak-size/body-weight regressions for *Vampyroteuthis infernalis* were obtained from specimens of local collections. Unidentified cephalopods were omitted from the quantification as they represented only a minor portion of the diet (four small, infrequent species in eight stomachs).

In order to approximate normal shark feeding times, digestive rates for captive sharks were determined and then compared with field data on the

digestive states of anchovies recovered from wild sharks. Three healthy, active sharks were acclimated for 24 h in large seawater holding tanks (14°-16°C) at Marineland of the Pacific, and then fed marked anchovies and market squid. Stomach contents were examined at 6, 12, and 24 h after feeding and the digestion rates recorded.

Short-term movements of sharks were monitored in the fall and winter seasons by telemetric instrumentation similar to those of Ferrel et al. (1974) and Nelson (1974). Transmitters were applied externally to free-swimming sharks with stainless-steel darts. Effective transmission range was approximately 2 km under good conditions but depended largely upon ambient noise from waves, wind, and biological sources. Some transmitters included a depth sensor for a record of vertical movements. Signals were tracked using a tuneable ultrasonic receiver and a staff-mounted directional hydrophone. These trackings supplement the spring through fall trackings of Sciarrotta and Nelson (1977).

The feeding behavior of blue sharks among spawning squid was studied in January 1976. Just before sunset, squid schools were detected near the bottom (30-40 m deep) using a recording Fathometer[4] and the work boat anchored directly above. A 1,500-W light was then suspended over the water. Squid typically converged beneath the light and formed a large surface school at which sharks usually appeared and began to feed.

Orientation and feeding responses of sharks to moving prey were documented during baiting sessions at offshore stations. In these tests, a dead anchovy, attached to a light fishing line was cast beyond the bait-attracted sharks and then retrieved back towards the boat. All field observations of shark and prey activities were made from the boat, using scuba and/or by snorkeling.

RESULTS

Sharks were captured during all months of the 1-yr study. Of the 81 sharks sampled, 94% had recognizable food items in their stomachs. The northern anchovy, *Engraulis mordax*, was the predominant prey item for sharks in the study area while other small fishes occurred at much lower frequencies (Figure 3).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Although sharks fed on a wide variety of cephalopods, an analysis of relative importance (Table 1) showed *L. opalescens* and squid of the genus *Histioteuthis* as the most common and substantial cephalopod prey. Monthly analysis revealed important shifts between these prey items

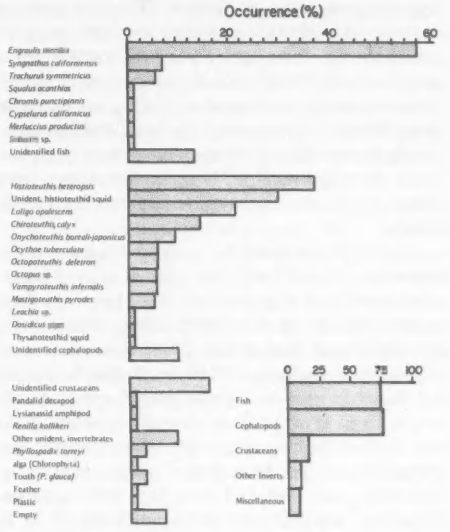

FIGURE 3.—Stomach contents of 81 blue sharks sampled during the year. Occurrence = percent of the 81 individuals containing that prey species. Inset gives a summary by broader food categories.

TABLE 1.—Annual relative importance of identified cephalopod prey in the diet of blue sharks near Santa Catalina Island, Calif. Importance was estimated as an index of relative importance (*IRI*) in accord with Pinkas et al. (1971): $IRI = (N + V)F$, where N (numerical percent) is the percent of individuals of that species among all individual cephalopods recovered; V (volumetric percent) is the percent volume represented by that species of all cephalopods recovered; and F (frequency) is the percent of individual shark stomachs containing that prey species.

Rank	Species	*F*	*N*	*V*	*IRI*
1	*Loligo opalescens*	21.0	70.6	31.9	2,152.5
2	*Histioteuthis heteropsis*	37.0	11.4	10.4	806.6
3	*Histioteuthis* sp.	23.5	5.0	.3	124.6
4	*Chiroteuthis calyx*	14.8	5.3	1.4	99.2
5	Thysanoteuthid squid	1.2	.2	43.3	52.2
6	*Onychoteuthis boreali-japonicus*	8.6	2.4	3.6	51.6
7	*Vampyroteuthis infernalis*	4.9	.8	2.2	14.7
8	*Octopoteuthis deletron*	6.2	1.0	.8	11.2
9	*Dosidicus gigas*	1.2	.2	5.1	6.4
10	*Ocythoe tuberculata*	4.9	.8	.4	5.9
11	*Mastigoteuthis pyrodes*	3.7	.6	.3	3.3
12	*Octopus* sp.	4.9	1.4	.2	7.8
13	*Leachia* sp.	1.2	.2	.004	.3

(Table 2). The high index for *L. opalescens* in January 1976 reflected the squid's extensive winter spawning assemblages in the study area, and similarly is the reason for its high annual rank (Table 1). Histioteuthid squid were probably the most significant cephalopod prey for sharks in more oceanic waters away from inshore spawning aggregations of *L. opalescens*. The low average number of anchovies and histioteuthid squid per stomach and the relatively small coefficients of dispersion for these two prey indicate that sharks obtained them somewhat regularly over a wide area (Table 3). Conversely, the large coefficient for market squid during its spawning season concurs with observations that this prey was taken from large schools during its spawning runs at inshore areas.

Digestive rate tests for healthy, captive sharks were in order with digestive states of prey recovered from wild sharks. Anchovies removed from captive sharks at 6 h after feeding were easily identified, and showed only preliminary digestion of fins and margins of the opercula. Likewise, whole squid were easily recognized and had only slight signs of external surface decomposition. At 12 h after feeding, digestion of anchovies was characterized by decomposed abdominal walls, moderate scale loss, and some skin deterioration. Digestion of squid was still negligible. At 24 h, anchovies were well digested with only vertebrae, otoliths, and small sections of muscle present. Squid heads were separated from the body and lenses had detached from the optic cups, but beaks were still implanted within the buccal mass. In general, digestive rates were at least twice as fast for anchovies than for squid.

Times of normal feeding activity were estimated by comparing the digestive rate data obtained from captive sharks with recognizable anchovies recovered from wild sharks. Anchovies that were freshly ingested predominated in sharks captured in early morning hours (Figure 4) and corresponded to a duration of approximately 0-8 h after ingestion. Moderately digested anchovies were prevalent in sharks sampled in the afternoon and represent anchovies held about 9-20 h after consumption.

Tooth marks on anchovies recovered from wild sharks indicate that prey were almost exclusively captured from behind. When present, tooth marks were usually located on the posterior lateral one-third of the anchovy, and in many cases impressions penetrated only the skin and not the myotome.

The movements of four sharks were monitored using ultrasonic telemetry in the winter (October-February) and supplement the spring, summer, and fall trackings of a previous study in the same area (Sciarrotta and Nelson 1977). Sharks ranged over wide areas (e.g., approximately 50 km² in 18 h: Tracking 2) and did not exhibit movements oriented towards the island shore. Vertical movements, except for the initial plunge immediately following tag application, were confined to the upper 15-m depth range.

TABLE 3.—Dispersion of the three major prey species in blue shark stomachs off Santa Catalina Island, Calif. Means for market squid were computed for squid spawning season (Mar. 1975, Dec.-Jan. 1976) and nonspawning season (Apr.-Nov. 1975, Feb. 1976). Coefficients of dispersion (ratio of variance to mean) indicate grouping of prey among stomachs. A coefficient of 1 describes a random distribution. Larger coefficients describe increasingly contagious (clumped) distributions of prey among shark stomachs (Sokal and Rohlf 1969).

Prey item	No. of sharks sampled	Mean no. prey per stomach	Coefficient of dispersion
Anchovies	81	1.06	1.92
Histioteuthid squid	81	1.52	2.68
Market squid:			
Spawning season	29	11.52	162.57
Nonspawning season	52	0.423	6.81

TABLE 2.—Monthly index of relative importance (*IRI*) of identified cephalopod prey in stomachs of blue sharks near Santa Catalina Island, Calif. See caption of Table 1 for calculation of *IRI*.

Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
Loligo opalescens	1,596	—	—	392	21	378	1,597	9,571	—	1,098	11,564	—
Histioteuthis heteropsis	780	17,369	3,917	6,454	166	9,406	2,298	254	—	1,376	370	—
Histioteuthis sp.	21	440	1,596	—	234	275	1,800	102	1,625	388	—	4,000
Chiroteuthis calyx	—	429	—	—	67	1,318	783	1,259	6,395	1,174	—	—
Thysanoteuthid squid	—	—	—	—	—	—	—	—	—	1,561	—	—
Onychoteuthis boreali-japonicus	68	—	—	—	169	—	—	—	—	1,188	23	—
Vampyroteuthis infernalis	—	—	—	—	130	—	521	—	—	136	—	—
Octopoteuthis deletron	40	—	1,373	—	19	—	—	—	—	55	—	—
Dosidicus gigas	—	—	—	—	216	—	—	—	—	—	—	—
Ocythoe tuberculata	14	—	—	—	23	—	138	—	—	47	—	—
Mastigoteuthis pyrodes	—	—	—	—	—	—	—	—	1,825	189	—	—
Octopus sp.	—	—	—	—	142	—	—	102	—	50	—	—
Leachia sp.	—	—	—	—	14	—	—	—	—	—	—	—

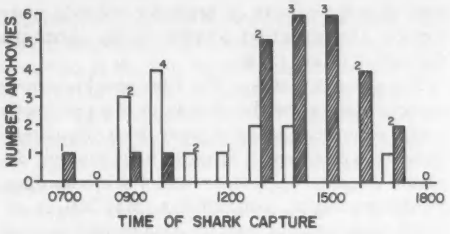

FIGURE 4.—Frequency of digestive states of anchovies in relation to time recovered from wild blue shark stomachs. Freshly ingested (light bars): anchovy body, scales, skin, and fins intact; represent anchovies about 0-8 h after ingestion. Moderate digestion (hatched bars): anchovy with head detached, open body cavity, and exposed myotome; represents anchovies about 9-20 h after ingestion. Advanced digestion (identification of anchovy possible only by vertebrae or otoliths) not included in distribution because of broad time span represented by this state (about 20 h or longer). Numbers indicate sharks sampled that contained anchovies in freshly ingested or moderately digested states. Water temperatures in the field ranged from 13° to 19°C.

Free-swimming sharks responded to moving prey (bait on slowly retrieved light fishing line) with a consistent posterior orientation, as illustrated in my field notes: "As I retrieved the bait towards the boat, a 1.5-m male shark sighted the anchovy and then swam in a wide arc so as to approach the bait from behind. He then made a rapid posterior-oriented dash up to the anchovy, bit the bait once at mid body, and swallowed it whole." Replicate tests using Pacific mackerel elicited similar posterior attacks; in these cases, the shark rolled partially on its side to take the larger fish prey. Tooth marks on bait in these test situations were similar to those on anchovies recovered from stomachs of wild sharks.

Sharks also showed several distinct patterns of predatory behavior while feeding on schools of spawning squid. Each feeding pattern appeared to be correlated with the size and level of activity of each shark as well as the physical configuration and alertness of the squid within the school. Surface and underwater observations of sharks feeding on night-light attracted squid revealed four feeding responses:

1) SLOW HEAD SWAYING: This feeding behavior was most common among larger sharks moving either through the center of moderately dense squid schools, or at the periphery of large, more diffuse aggregations. Sharks swam among the squid at a relatively slow speed, with pronounced lateral head movements and corresponding broad tail sweeps. Squid were generally captured in the corners of the mouth and swallowed whole. In this behavior, sharks did not show rapid head shaking (as often occurs when sharks bite on relatively large prey) although lateral head jerks to position prey for swallowing were common. Sharks moved in a relatively straight path, and created minimal disturbance to the school.

2) TURNING: Turning behavior was most frequent among sharks feeding at the surface when squid were in an alert state or not in tight schools. As the shark approached the school, the squid (which swam backwards and could view the predator's approach) began to turn in tight arcs away from the shark's path. The shark would respond by turning in an accelerated pursuit, but was most often eluded by the squid. Sharks that were successful quickly whipped their heads to one side and captured squid in the corner of their mouths.

3) CHARGING: This behavior can best be described as a straight accelerated rush through a dense school of squid. Charging was most prevalent among the more active sharks that had just arrived at a squid congregation. Typically, the shark showed no orientation to specific individuals, and indiscriminately engulfed large numbers of prey.

4) TAIL STANDING: Sharks also fed on the lower portions of squid schools. As previously described, squid would often be concentrated directly beneath the light source so as to form a dense school. In this feeding behavior, the shark first circled the lower portion of the school and then moved up to the squid and assumed a near vertical attitude, using broad tail sweeps to maintain position. Then the shark lunged its head into the bottom of the school and engulfed many individual squid. The longest duration of a tail-standing posture was 20 s in which approximately 30 squid were consumed by one individual. This behavior was observed only when squid schools were most dense and was not as common as other feeding modes.

DISCUSSION

Blue sharks fed on a variety of small fishes and cephalopods associated with both pelagic and inshore habitats. Northern anchovies were the major prey for sharks in this investigation, and off Newport Beach, Calif. (Bane 1968), while small schooling fishes composed a major portion of blue

shark diets in other coastal areas of the world (Bigelow and Schroeder 1948; LeBrasseur 1964; Stevens 1973). Major concentrations of anchovies in the California Current system were centered in the semiprotected waters of the Southern California Bight (Mais 1974) which lies between Point Conception and Point Descanso, Mexico (approximately from lat. 32.0°N to 34.5°N, area of about 50,000 km²). The main portion of the southern California anchovy population was reported by Mais to be distributed within 37 km of the mainland over deep water (228.6-731.5 m) which includes the study area at Catalina.

The most prevalent schooling behavior for anchovies in deep open waters (bottom depth >183 m) was the formation of small (4-15 m thick), near-surface daytime schools (0-54.9 m deep) that dispersed at night into a thin surface scattering layer (Mais 1974). Field observations from the present study indicate a similar behavior for anchovies near Catalina. In offshore waters during the day, anchovies occurred in large, dense, polarized schools near the surface. In the early evening, schools dispersed horizontally into less dense feeding assemblages with individuals spaced approximately 0.5 m apart. Later at night (0100-0400 h) more dispersed groups and solitary individuals were observed on several occasions, indicating a more complete nocturnal dissolution.

In spite of the abundance of this prey no sharks examined near Catalina had stomachs distended with anchovies; usually only one or two had been taken per day. Data from the digestion studies indicate that most predation on anchovies occurred in predawn hours which correlates with the increased nocturnal activity of telemetered sharks reported by Sciarrotta and Nelson (1977). It seems probable then, that the few anchovies taken by each shark was at least partially due to the nocturnal dispersion of schools in offshore waters, whereby assemblage densities were reduced and anchovies taken individually.

The localized variability of anchovy abundance and schooling behavior that existed between areas and seasons presented different feeding opportunities for sharks. For example, blue sharks captured during the day off Newport Beach, Calif., and in commercial anchovy fishing grounds near Los Angeles Harbor (author unpubl. data) contained many more anchovies (approximately 10-20/individual) than did sharks sampled in the Catalina study area. The two former areas feature nearshore submarine escarpments where the size and concentrations of anchovy schools were among the greatest anywhere in southern California (Mais 1974).

The present status of the blue shark-anchovy association may be the aftermath of a previously more complex predator-prey web. Southern California commercial fisheries have severely depleted *Scomber japonicus* and Pacific sardine, *Sardinops sagax*, populations (MacCall et al. 1976), both natural prey for blue sharks (author unpubl. data). Although such declines in major forage species may have resulted in increased predation on anchovies, the southern California population is apparently in little danger of overexploitation by commercial fisheries or pelagic fish predators (Pinkas et al. 1971; Mais 1974; MacCall et al. 1976).

Fishes associated with inshore habitats were also taken by sharks. Jack mackerel, *Trachurus symmetricus*, are widely distributed throughout the Gulf of Alaska (Miller and Lea 1972), and inhabit both inshore and pelagic habitats (Feder et al. 1974). In southern California waters, adults of this species generally aggregate near the bottom or under kelp forests at rocky banks and shallow coastal areas during daylight and venture into deeper waters at night. Only rarely do jack mackerel form sizeable surface schools in the open sea (Mais 1974). Similarly, smaller jack mackerel (e.g., near 25 cm TL), common at inshore areas of Catalina, swam along the outer edges of kelp beds during the day in closely spaced schools and sometimes aggregated within the kelp forest proper. At night jack mackerel occurred in open waters (away from kelp) often interspersed with *Scomber japonicus*. Larger pelagic individuals might represent a schooling prey source for blue sharks in open waters, but stomach content data indicate this was not the case near Catalina. Neave and Hanavan (1960) described concurrent expansion of blue shark and jack mackerel ranges in the Gulf of Alaska during the summer, although no data was presented on possible predator-prey interactions.

Pipefish were the second most frequent fish prey for sharks in this study and a principal prey for blue sharks off Newport Beach (Bane 1968), but because of their small biomass must be regarded as a prey species of minor importance. Free-swimming pipefish were observed at the surface in open water (far from surfgrass or kelp beds) at night, among flotsam kelp during daylight, and during daytime scuba dives in kelp forest and

surfgrass, *Phyllospadix torreyi*, habitats along the shore of the island. The occurrence of pipefish at the surface in the San Pedro Channel at night and the fact that sharks containing freshly ingested pipefish were captured 2-5 km from the island imply that this prey was most likely taken in waters away from inshore kelp and surfgrass habitats.

Freshly ingested blacksmith, *Chromis punctipinnis*, were recovered from a shark captured near Ship Rock at noon. At Catalina, this planktivorous damselfish formed midwater feeding aggregations at the outer edges of the kelp forest during the day, and at times ranged seaward up to 100 m from the nearest kelp. At dusk, blacksmith retreated to the protection of rocks and crevices (see Quast 1968; Hobson 1976). Blue sharks frequented waters near exposed kelp stands at Ship Rock and have been reported chasing and feeding on blacksmith during the day (Sciarrotta and Nelson 1977; Given[5]).

With the exception of *Mastigoteuthis pyrodes*, *Vampyroteuthis infernalis*, and nonspawning *Loligo opalescens*, all of the cephalopod prey species (or their congeners for which data are available) occur near the surface at night through vertical ascent from greater depths or by normal epipelagic distribution (Roper and Young 1975; Tricas 1977). *Mastigoteuthis pyrodes* (mesopelagic) and *V. infernalis* (bathypelagic) occasionally migrate to the lower limits of the epipelagic zone at night (Roper and Young 1975).

In their study of blue shark movements near Catalina, Sciarrotta and Nelson (1977) described evening-twilight shoreward movements of sharks from late March through early June and suggested the change in movement patterns as a response to seasonal increases of inshore spawning squid and decreases in availability of pelagic fishes offshore. Such movements, however, may not be strictly food related. For example, daily inshore-offshore migrations of sharks (late March through early June) would not be synchronous with the cold-water winter peak (December through February) of inshore squid spawning activity near the Isthmus. Also, some sharks observed during this study fed among spawning squid schools throughout the day and therefore did not exhibit the diel inshore-offshore movement pattern. Furthermore, sharks fed upon anchovies in offshore waters throughout the year and there is no indication that the availability of anchovies or jack mackerel to blue sharks significantly changed over the course of this study.

Detection of prey by sharks is often dependent on the reception of abnormal or unusual stimuli such as low-frequency vibrations of struggling or fleeing fishes (Nelson and Gruber 1963; Nelson and Johnson 1972). In addition, olfaction plays a well-documented role in location of injured, stressed, or bleeding prey (Tester 1963; Hobson 1963). Ultimately, however, vision (Gilbert 1963) and possibly electroreception (Kalmijn 1971) are the principal senses used immediately prior to attack. For blue sharks in a normal nocturnal feeding mode, it is probable that search images are formed for a general size rather than for a particular species. Pipefish, for example, were relatively small in biomass, but represented a length characteristic of other prey species. Similarly, most cephalopods in the diet fell within the common prey size range (e.g., 5-25 cm TL). Bioluminescent trails of darting anchovies and other small fish and squid were frequently seen while snorkeling at night in offshore waters and likewise would be readily visible to sharks. Also, the majority of cephalopod species taken by sharks possessed photophores. Bioluminescence associated with prey movements and light organs may represent significant predatory cues for sharks at night.

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LIFE HISTORY AND VERTICAL MIGRATION OF THE PELAGIC SHRIMP *SERGESTES SIMILIS* OFF THE SOUTHERN CALIFORNIA COAST

MAKOTO OMORI[1] AND DAVID GLUCK[2]

ABSTRACT

Sergestes similis in the southern California eddy was observed with respect to reproduction, daily and ontogenetic vertical migrations, growth, and longevity. The period of highest spawning activity occurs between late December and early April, but small pulses of spawning are occasionally observed in late spring and summer. The release of eggs takes place close to shore above the continental slope, and then the eggs sink to 200 m or deeper. Nauplius larvae ascend and protozoeal and zoeal larvae stay mostly above 100 m. The daily vertical migration becomes evident after the second protozoeal stage. Adults are abundant between 50 and 200 m at night and 250 and 600 m in the daytime.

The spawning activity of *S. similis* becomes highest during the period when the vertical thickness of the optimum temperature zone (10°-15°C) is the greatest. The authors speculate that the local population off the southern California coast may be joined by the subarctic population. It is possible that multiple spawnings occur from females of the southern California population.

The lifespan of *S. similis* is 2.0-2.5 years for females and about 1.5 years for males. Sexual maturity is reached at about 1 year in both sexes. Females reproduce in two successive spawning seasons, and males seem to accomplish multiple fertilizations. Growth trends are similar to those reported for *S. similis* off Oregon. Growth rates are described using growth curves fitted by the von Bertalanffy and logistic equations.

Sergestes similis Hansen is the most abundant oceanic, pelagic shrimp in the North Pacific Drift, lat. 40°-50°N. This subarctic and transitional species occurs mainly in waters where temperature ranges between 3° and 13°C. Its distribution extends from Japan to the coast of North America as far south as lat. 27°N (Pearcy and Forss 1969; Omori et al. 1972).

In the cooler part of the California Current, *S. similis* composes a substantial fraction of all micronekton. The adults perform extensive vertical migrations, living between 250 and 600 m in the daytime and ascending to 50-200 m depths at night. According to Barham (1963) and Clarke,[3] *S. similis* is consistently associated with the lower component of a sonic scattering layer off southern California.

Sergestes similis sheds eggs in the sea. From eggs hatch the first of four naupliar stages (N1-N4), which go on to develop three protozoeal stages (PZ1-PZ3), and two zoeal stages (Z1, Z2) before entering postlarval stages (PL) (Omori 1979).

Sergestes similis plays an important role in the dynamics of northern Pacific oceanic ecosystems. As an adult, it feeds mainly on copepods and euphausiids and is, in turn, preyed upon by squids, mesopelagic fishes, rockfishes, albacore, basking shark, and baleen whales (Pereyra et al. 1969; Judkins and Fleminger 1972; Omori et al. 1972; Mutoh and Omori 1978). In certain areas there is a strong possibility that the enormous standing stock can be exploited by commercial fisheries (Omori 1974).

In spite of the great importance of this species, little is known about its life history, especially its reproduction, development, and growth. Although the distribution and daily vertical migration of adult *S. similis* off the coasts of California and Oregon have been studied (Barham 1963; Clarke, see footnote 3; Pearcy and Forss 1966; Davies and Barham 1969; Pearcy et al. 1977), no work has been done on the biology of larval and early postlarval stages. Details of the spawning season and lifespan of the species have not yet been confirmed. Barham (1957) stated that *S. similis* in Monterey Bay, Calif., reached maturity at age 1 yr and dis-

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appeared after spawning. He found that the two size-groups, which spawned in December-January and June-July, respectively, showed the same developmental history but 6 mo out of phase with each other. On the other hand, *S. similis* off the Oregon coast spawned during most of the year but predominantly during the winter and spring, with the individuals living for about 1 yr (Pearcy and Forss 1969). Genthe (1969) determined that the lifespan for the southern California population is 2 yr and that the maximum breeding activity occurs in the early summer and fall. The disagreement in these conclusions is mainly due to two factors: first, the difficulty of sampling a nonrandomly distributed population which moves both horizontally and vertically with time and spatial location; and second, the lack of knowledge about the developmental biology of the larval stages of *S. similis*. Knowledge of the development and growth of larvae and juveniles of *S. similis* has been severely restricted by the difficulties of maintaining this oceanic species under laboratory conditions. Recently, however, Omori (1979) has successfully reared this species from the egg to the eighth postlarval stage. This success prompted us to examine the life history of *S. similis* off southern California and to provide further biological information about its population dynamics.

The present study deals with the reproduction, growth, longevity, and both daily and ontogenetic vertical migrations of *S. similis*. The study area is the southern California eddy, which is bounded on the north by Point Conception, lat. 34°N, and on the south by about lat. 30°N. The east-west extent of the eddy is about 250 km. This region is the southernmost in which *S. similis* is abundant. The sluggish, cyclonic circulation of this eddy, defining a singular water mass, permits substantial autonomy for the resident population. Complex topography, including a scattering of islands, basins, and canyons in the area, appears to provide substantial swarming grounds for *S. similis*. Because the majority of the population resides in an area such as the southern California eddy, which Brinton (1976) has described as "hydrographically restricted," data on the life history of *S. similis* may be measured more easily than in other oceanic areas.

MATERIALS AND METHODS

In the present study, data on occurrence of the larvae and early postlarvae were determined from examination of California Cooperative Oceanic Fisheries Investigations (CalCOFI) samples.

Samples were obtained from selected stations in CalCOFI cruise 6401 (January-February 1964). Stratified plankton sampling was carried out along three parallel transects: Line 60, Line 90, and Line 100 (Figure 1). The samples were collected by oblique tow to various depths of water with a standard CalCOFI net of 1-m diameter and 0.55-mm mesh openings (Ahlstrom 1948). The mesh size of the cod end and the 40-cm section in front of it was 0.25 mm. Opening-closing net series were obtained to depths of approximately 100 m at three stations and 450 m at one other station on Line 60, and to depths of 400-600 m at all stations on Line 90. Sampling was carried out at whatever time of day the ship arrived on station. Both day and night series, to approximately 600 m depth, were obtained at all station on Line 100. In the present study the samples obtained from the usual habitat of *S. similis*, i.e., above 400 m depth, were examined (Table 1). At each station, usually two to six nets were towed in each of two or three series of tows. The opening and closing of the nets were messenger-activated, using a Leavitt-type device, and a flowmeter was mounted within the mouth of each net. A net filtered an average volume of about 600 m^3/tow. A trace of depth vs. time was made during the course of a tow by a recorder attached near the bottom net. For a detailed description of the sampling procedure and the analysis of depth recorder traces, see Brinton (1967).

The spawning season of *S. similis* was determined by examining CalCOFI standard oblique haul samples obtained at Stn. 90.37 from January 1951 to December 1954. Station 90.37, lat. 33°11′N, long. 118°37′W, was selected because it was located near the center of *S. similis* larval distribution in CalCOFI 6401. Sampling was not conducted in October and December 1952, May, September, and November 1953, and June and September 1954, but sampling from a nearby station, 90.35, was done in May 1953. Details of this sampling method are described by Ahlstrom (1948) and Fleminger (1964). The net was towed obliquely between the surface and a depth of about 140 m while the ship proceeded at a speed of about 2 kn. As explained later, this sampling depth covered the entire vertical distribution of protozoeal and zoeal stages of *S. similis*. Because free eggs and nauplii of *S. similis* are <0.5 mm, they were not retained by the CalCOFI net. Specimens of protozoeal stages were retained by the fine meshes

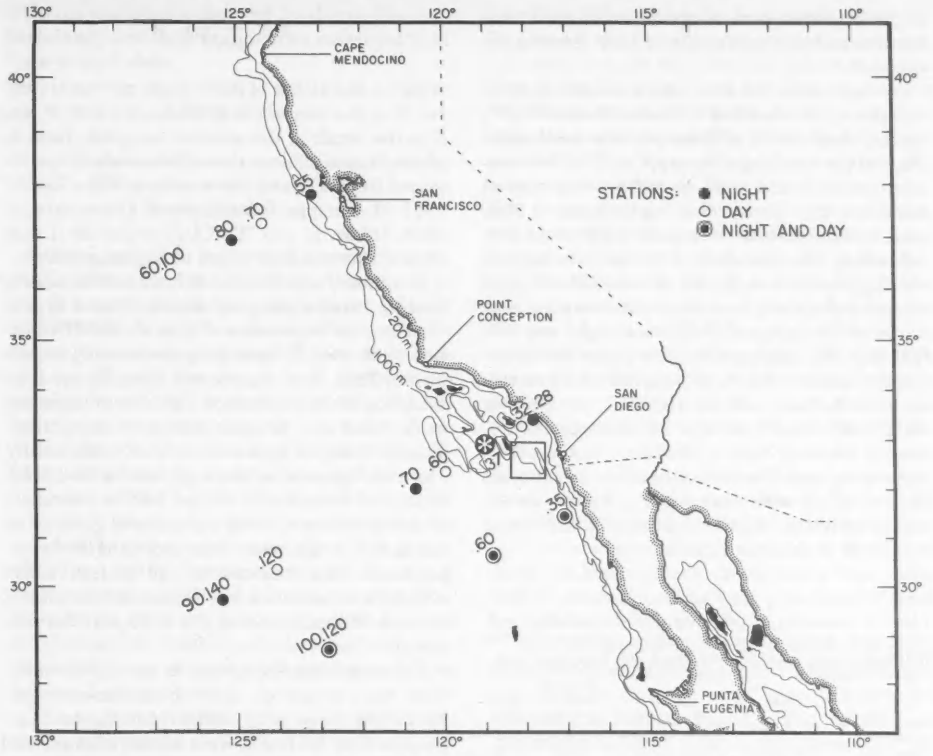

FIGURE 1.—Sampling stations for *Sergestes similis* off southern California. Circles indicate stations sampled by stratified opening-closing oblique net hauls with CalCOFI net (CalCOFI 6401, January-February 1964). Line 60 (Stn. 60.55, 60.70, 60.80, and 60.100) extending southwestward from Pt. Reyes, Calif.; Line 90 (Stn. 90.28, 90.32, 90.37, 90.60, 90.70, 90.120, and 90.140) extending southwestward from Dana Pt., Calif.; and Line 100 (Stn. 100.35, 100.60, and 100.120) extending southwestward from Punta Banda, Baja California. Number 37 (flowered circle) marks Stn. 90.37 at which monthly CalCOFI standard oblique haul samples were obtained. The square indicates the area of IKMT trawls.

TABLE 1.—Summary of data from stratified plankton sampling off southern California with standard CalCOFI net (CalCOFI cruise 6401, January-February 1964).

Station	Period	Depths covered by series of tows	Number of stratified samples	Date	Towing times including 2-3 series of tows	Light condition
60.55	Night	0-108	3	31 Jan.	2316-0056	Dark
60.70	Day	0-450	10	1 Feb.	1241-1455	Clear
60.80	Night	0-72	4	1 Feb.	2024-2044	Dark
60.100	Day	0-108	6	2 Feb.	0829-1003	Clear
90.28	Night	0-80	4	6 Feb.	0342-0407	Clear, ½ moon
90.32	Day	0-140	8	6 Feb.	0854-1052	Clear
90.60	Day	0-373	8	7 Feb.	1053-1346	Clear
90.70	Night	0-100	5	7 Feb.	2044-2149	Dark
90.120	Day	0-490	8	9 Feb.	1345-1640	60-90% clouds
90.140	Night	0-132	6	9 Feb.	2330-2356	Dark
100.35	Night	0-236	7	16 Feb.	2242-0106	Dark
	Day	0-400	9	17 Feb.	0715-0903	Clear
100.60	Night	0-260	8	16 Feb.	0041-0300	Dark
	Day	0-355	9	16 Feb.	0930-1140	95% clouds
100.120	Night	0-185	5	14 Feb.	0203-0538	Dark
	Day	0-500	8	14 Feb.	1051-1302	60% clouds

of the posterior part of the net and were thus counted as being indicative of their general occurrence.

Juvenile and adult *S. similis* were collected by a 6-ft (1.8-m) Isaacs-Kidd Midwater Trawl (IKMT), having mesh width of 2 mm, on the continental slope of the San Diego Trough, Calif., at five occasions in 1976 and 1977. Sampling was done at night and daytime by releasing the cable at 50m/min until the net reached a desired depth and then retrieving. Ship speed was 4 kn while the net was sinking, and 2 kn during the retrieval. Usually the biomass of shrimp was large when the net was towed at the depths of 50-200 m at night and 250-600 m in the daytime. To fill in gaps where sampling was sparse and to provide more information on reproduction and growth of *S. similis*, six IKMT collections from the SIO (Scripps Institution of Oceanography) Invertebrate Collection were examined. These samples were all collected by 10-ft IKMT with mesh width of 5 mm between lat. 32°28′N and 33°15′N and long. 117°29′W and 118°38′W (Table 2).

TABLE 2.—Summary of data from sergestid sampling with Isaacs-Kidd Midwater Trawl off southern California. Six-foot IKMT with 2-mm mesh size; 10-ft trawl with 5-mm mesh size.

Date	Local time	Location Lat.	Long.	Estimated depth of haul (m)	IKMT (ft)
26 Jan. 1977	1915-1935	32°44′N,	117°30′W	0-200	6
3 Mar. 1977	1810-1836	32°43′N,	117°29′W	0-250	6
12 Apr. 1972	2206-2345	33°15′N,	118°38′W	0-500	10
21 Apr. 1977	0332-0414	32°47′N,	117°29′W	0-300	6
21 June 1953	1601-1937	32°37′N,	118°10′W	0-1,490	10
27 July 1973	1725-2320	32°28′N,	117°58′W	0-800	10
19 Aug. 1976	1800-1830	32°41′N,	117°29′W	0-300	6
24 Aug. 1954	2400-0400	32°40′N,	117°35′W	0-549	10
28 Oct. 1972	1800-1900	32°45′N,	117°30′W	0-500	10
29 Oct. 1976	2000-2100	33°10′N,	118°20′W	0-350	6
8 Nov. 1975	1600-?	32°36′N,	117°20′W	0-500	10

An aliquot of ¼ to 1/32 of each CalCOFI sample was examined, and the number of individuals of each developmental stage from the first protozoeal stage to the second zoeal stage was counted. Postlarvae having a body length (BL) <5.0 mm (stages I-VI) were classified together as early postlarvae. In order to increase accuracy, if the initial aliquot contained only two or fewer individuals of any particular stage, a second aliquot of equal size was examined for specimens of that stage. All counts were then standardized for 1,000 m^3 of water filtered by the net. An estimate of the total number of individuals of each stage beneath 1 m^2 of sea surface was made using the equation,

$$n = \frac{N}{1000} \times d$$

where n is number of individuals per square meter, N is the number of individuals/1,000 m^3, and d is the depth of the stratum sampled. Data on physical and chemical environments were obtained from "Oceanic observations of the Pacific" 1951-53 (Scripps Institution of Oceanography 1963, 1965a, b) and "CalCOFI cruise 6401 data report" (Scripps Institution of Oceanography[4]).

In January and March 1977, a small number of healthy females carrying well-developed eggs in their ovaries were removed from the IKMT collection to be used for spawning and rearing experiments. They were transferred immediately after sampling to chilled filtered seawater in large containers and were brought back to the laboratory. The spawning of eggs was observed individually. The sinking speed of the eggs over a 70-cm distance was measured at 10° and 14°C in a constant temperature room using a graduated glass cylinder of 70-mm diameter. Seawater used for the experiment was obtained at the station where ovigerous females were collected. It was filtered through Millipore[5] filters HA (0.45 μm). Salinity was 33.72‰.

The remaining specimens in the IKMT collections were preserved in 5% Formalin-seawater. Most specimens of *S. similis* having carapace lengths (CL) >5.0 mm were sorted, counted, and sexed. The carapace length from the tip of the rostrum to the posterior margin of the carapace at the dorsal midline was measured to the nearest 0.5 mm.

Change through time in the carapace length-frequency histograms of *S. similis* was graphically analyzed using probability paper (Harding 1949; Cassie 1954). In order to compare the growth trends of the *S. similis* population off southern California with trends in other waters, previous data on the size-frequency distribution of *S. similis* reported by Genthe (1969), Pearcy and Forss (1969), Omori et al. (1972), and Mutoh and Omori (1978) were reanalyzed to obtain average or modal carapace lengths[6] for the populations at

[4]Scripps Institution of Oceanography. 1965. Physical and chemical data CalCOFI cruise 6401, 10 January-4 March 1964. SIO Ref. 65-7, 76 p.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6]BL/CL regression of *Sergestes similis* (>5.5 mm CL) are as follows:

different sampling dates and locations. The von Bertalanffy and logistic equations were used to fit these growth data.

RESULTS

Daily and Ontogenetic Vertical Migrations of Larvae and Early Postlarvae

Coastal upwelling is generally weak in southern California during the winter (Bakun 1973). This is consistent with the data on environmental properties at the sampling stations (Figure 2). The thermocline remained at about 75 m at all stations on Line 60 with the mixed layer temperature ranging from 11.5°C inshore to 14.0°C offshore. Salinity was usually <33.30‰ in water above 75-m depth. On Line 90, except for the two outermost stations, the thermocline was at 30-50 m and the temperature within the mixed layer was >13.5°C. Salinity was >33.20‰ at all depths. On Line 100 the thermocline was at about 50 m at Stn. 100.35 and 100.60. Temperature within the mixed layer was about 15°C, and salinity was >33.50‰. The position of the oxycline coincided with that of the thermocline at nearly all stations. Generally, the oxygen level at depths below the mixed layer increased going seaward.

The main population of *S. similis* larvae was always between the surface and 100-m levels, and they occurred in greater abundance at stations on the continental slope (Figure 3). The population density was highest at Stn. 90.32 (101 individuals/m²). The larvae did not occur at Stn. 90.120, 90.140, and 100.120. In these southern offshore stations the temperature above 100 m was >16°C. The temperature-salinity curves characterized the water mass as eastern North Pacific Central water, where *S. similis* has never been found. In this water mass, the "ortmanni type" larvae (the *Sergestes corniculum* group, see Yaldwyn 1957 and Omori 1974) were commonly distributed.

The vertical distributions of larvae and early postlarvae from eight stations where they were abundant shows that the larvae were scattered from 20 to 100 m during the daytime (Figures 4, 5). On Line 90, the distribution pattern did not coincide well between the stations closest to shore (Stn. 90.28 and 90.32) and the offshore stations (Stn. 90.60 and 90.70). At Stn. 90.60 in the daytime, the larvae were widely distributed throughout the 0-110 m layer, but larvae occurred only between 44 and 88 m at Stn. 90.32 during the day. The greatest population density observed was within the 66-88 m layer at Stn. 90.32 (about 3,500 individuals/1,000 m³). Nighttime larval distribution was between 20 and 90 m at Stn. 90.70, but again, it was below 40 m at the closest inshore station. A similar inshore and offshore assemblage was observed along Line 100, although the vertical distribution of the larvae was expanded more widely. At Stn. 100.35 the larvae were most abundant between 50 and 100 m in the daytime and 0 and 80 m layer at night. On the other hand, at Stn. 100.60 the main population in the daytime occurred between 20 and 120 m, while at night the distribution ranged from the surface to 140 m with considerable numbers in the 0-40 m layer. At both stations, there was a clear daily vertical migration of the main population of zoeal and postlarval stages.

With the present sampling method, there was some doubt whether the same population was measured by day and night tows. However, as indicated in Figures 4 and 5, the estimates of abundance beneath 1 m² of sea surface did not differ appreciably between day and night at the two closest stations on Lines 60 and 90 and between day and night tows at the same station on Line 100. It can be said, at the least, that the avoidance of nets by larvae in the daytime was no greater than at night.

When abundance vs. depth is combined and averaged for each larval stage at each station, the extent of daily vertical migration becomes clear. The first protozoeal stage shows at least a restricted daily vertical migration (Figure 6). The larvae gradually increase their range of vertical distribution with growth while gradually inhabiting deeper water. Thus, the main population of early postlarva (40-45 m at night and 70-75 m in the daytime) shows a deeper distribution than earlier larval stages.

Eggs of *S. similis* (about 0.3 mm in diameter) were slightly heavier than the density of the experimental water; the difference in sinking rates was not significant at the 5% level between 10° and 14°C under laboratory conditions (Table 3).

BL = 3.15 + 2.85 CL for females,
BL = 2.55 + 3.11 CL for males (Omori et al. 1972).
The regression for juveniles with carapace length 5.5 mm or less is:
BL = 3.08 CL.

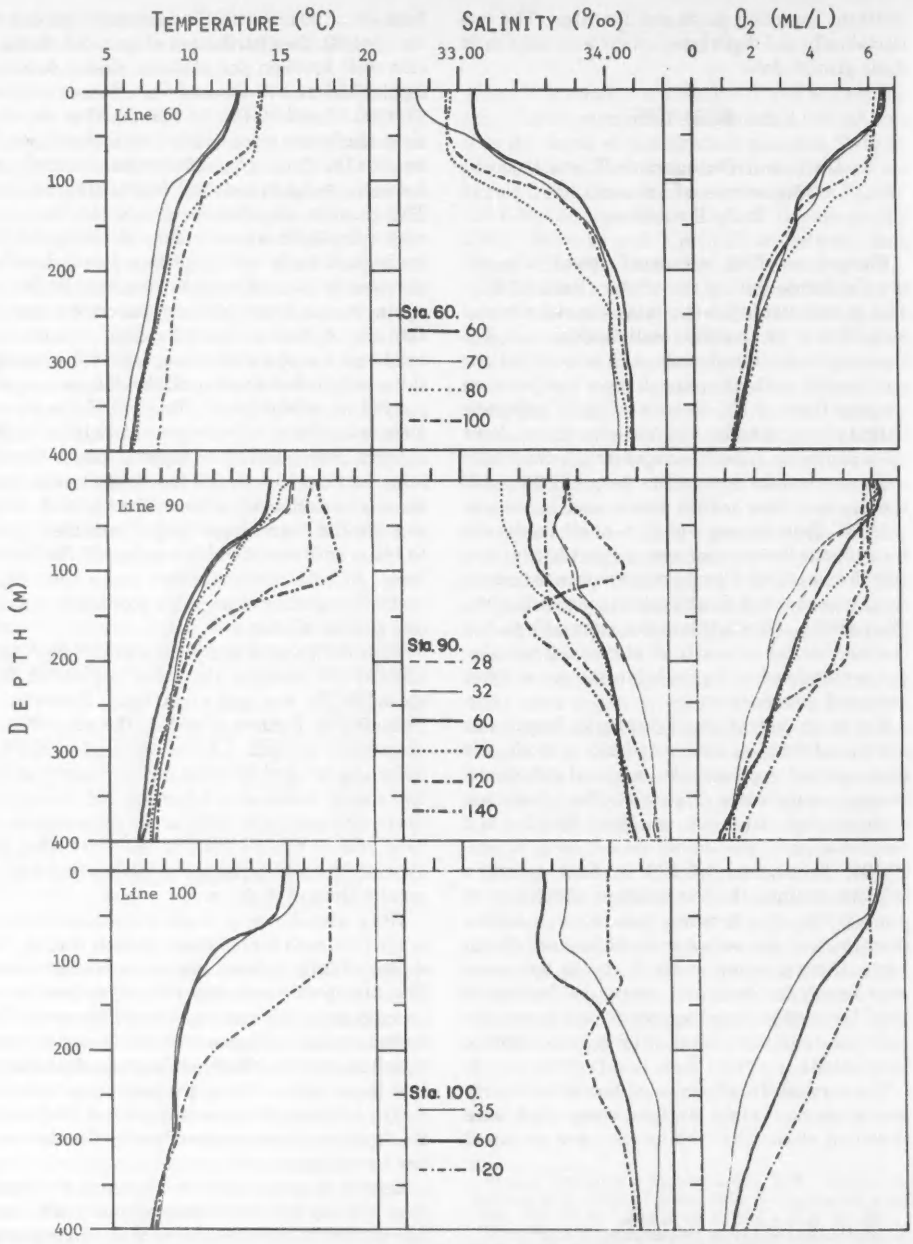

FIGURE 2.—Vertical profiles of temperature, salinity, and oxygen on CalCOFI Lines 60, 90, and 100, January-February 1964, off southern California.

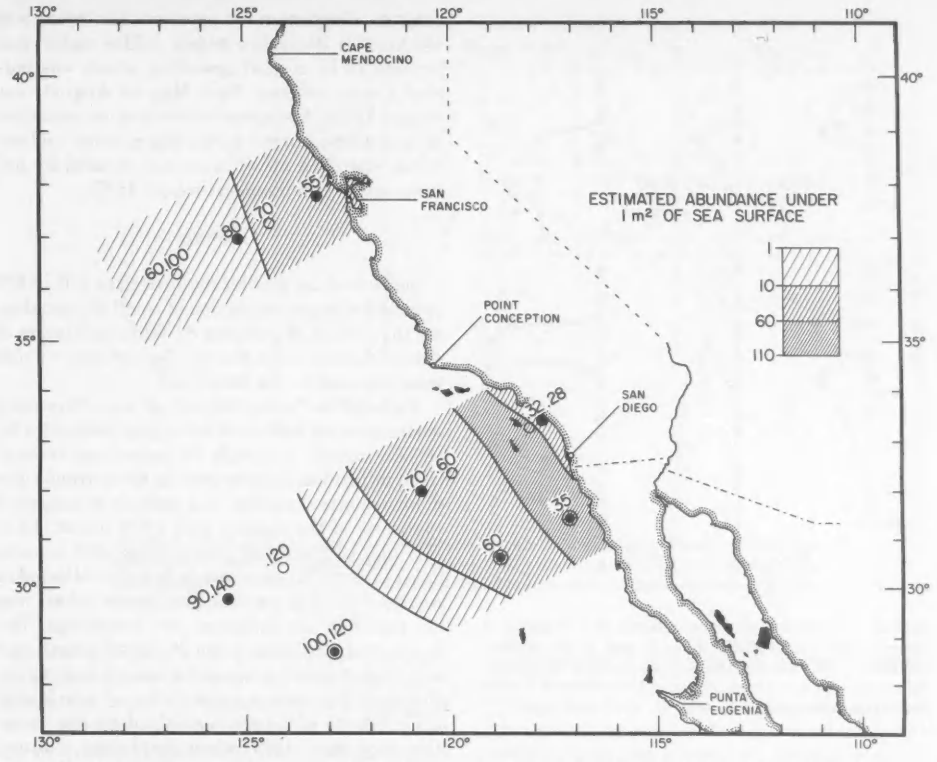

FIGURE 3.—Distribution and abundance of *Sergestes similis* larvae from January to February 1964. Estimated abundance is expressed as number of individuals beneath 1 m² of sea surface in depths between 0 and 100 m.

TABLE 3.—Experimental data on sinking velocity of eggs of *Sergestes similis* in water of salinity 33.72‰. Difference in sinking rates is not significant at the 5% level.

Temperature (°C)	Replicates	Sinking velocity (m/h)		
		Average	SD	Range
10	9	1.45	0.44	0.91-2.19
14	9	1.81	0.52	1.04-2.99

Spawning Season

The highest spawning of *S. similis* took place from late December to early April. Protozoea larvae occurred most abundantly between January and April at Stn. 90.37 (Figure 7), but were not found in samples collected in November and December. During 1951-54, a number of PZ2 and PZ3 appeared each year between January and July, but the occurrence of PZ1 was restricted to January-April, except for August 1952 and July 1954. Although one-third of the autumn months were not represented by samples, these months were scattered enough to make the data significant. Seasonal abundance of zoeal stages duplicated that of PZ1. Early postlarvae were found in plankton from February to early July. Considerable numbers of PZ1 and PZ2 (<1.3 mm BL) apparently passed through the mesh of the CalCOFI net, as their measured population densities were almost always lower than those measured for PZ3.

The optimum temperature range for larval development is 10°-15°C (Omori 1979), and the highest temperature at which adult *S. similis* occur is 13°C. Thus, the best temperature for the larvae is close to the upper temperature limit of the adult's habitat. Furthermore, comparison of the reproductive activity of *S. similis* with physical and

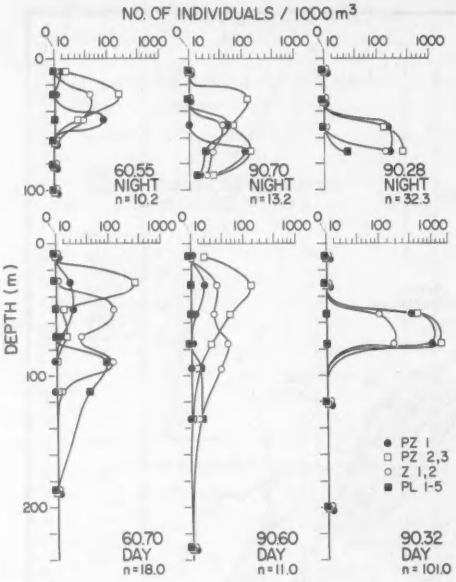

FIGURE 4.—Vertical distribution of larvae and postlarvae of *Sergestes similis* on CalCOFI Lines 60 and 90 off southern California. PZ, protozoeal stages; Z, zoeal stages; PL, postlarval stages. Estimated total number of larvae beneath 1 m² of sea surface indicated by n.

chemical environmental data indicates that there is a relationship between temperature and spawning season (Figure 7). Spawning activity was highest during the period when the vertical stratum of optimum temperatures for larvae was thickest. It decreased before colder water was brought in by coastal upwelling which was normally most intense from May to August (see Bakun 1973). A seasonal minimum, or cessation, of spawning occurred during the summer and autumn when the upper layer was covered by unfavorably warm temperatures (>15°C).

Growth

Because of the smaller mesh size, the 6-ft IKMT retained a larger proportion of small shrimp than did the 10-ft IKMT (Figure 8). While specimens of 4 mm CL occurred in the smaller net, few <7 mm were retained in the larger net.

Well-defined progressions of size-frequency modes gave indications of average growth rates for certain cohorts, although we sometimes encountered difficulties in interpreting these trends due to inadequate sampling, and possibly to extended spawning of the species. One 1975 cohort (12.0-14.5 mm CL) and two conspicuous 1976 cohorts (5.0-11.0 mm CL) were seen in females collected in August 1976 (Figure 8A). The former cohort was not found in the following two samplings. The large-sized 1976 cohort (mean modal length, 8.4 mm CL in August) reached 9.9 mm CL in October, 10.5 mm CL in January, and 11.8 mm CL in March 1977. Growth of the small-sized cohort was traceable until April 1977, when the shrimp attained an average carapace length of 10.4 mm. Recruitment of postlarvae <6.0 mm CL (1977 cohort) was intense in April. The histogram for March showed only a single mode of males, and it is not possible to

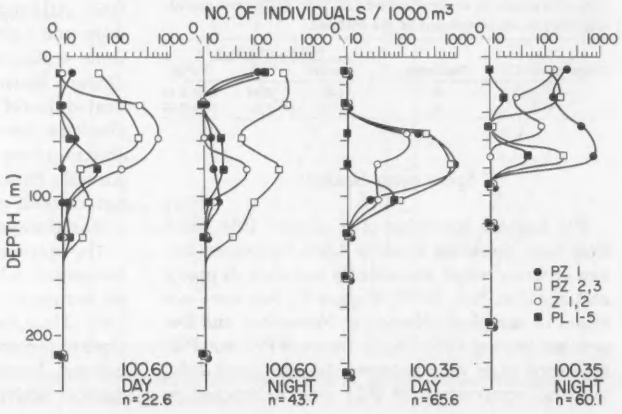

FIGURE 5.—Vertical distribution of larvae and postlarvae of *Sergestes similis* at CalCOFI Stn. 100.35 and 100.60 off southern California. Estimated total number of larvae beneath 1 m² of sea surface indicated by n.

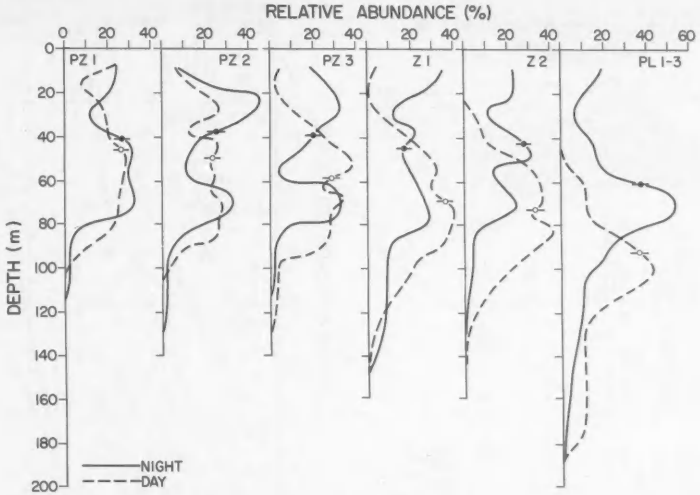

FIGURE 6.—Vertical distribution of larvae and postlarvae of *Sergestes similis* off southern California. Abundance vs. depth at all sampling stations was combined and averaged. Horizontal line indicates the depth at which the cumulative catch represented 50% of the total catch. PZ, protozoeal stages; Z, zoeal stages; PL, postlarval stages.

say whether this 1976 cohort represents the large-sized group or not. In the 10-ft IKMT samplings the most conspicuous female cohort of 10.5-13.0 mm CL in April reached 13.5-15.5 mm CL in October (Figure 8B). The males grew from an average 10.8 to 11.7 mm CL between April and August. In many cases, the size structure of the population showed the presence of only one or two obvious size groups, but in three cases (April 21, June 21, and July 29) the histograms of females indicated three size groups. Development of the smallest cohort of 0 age-group was traceable until August in both females and males, but in October and November, two cohorts of 0 age were apparent.

Some estimates of growth were attempted using changes in the average or modal lengths in various months. In order to show the growth trend more definitely, the results of all previous length measurements of *S. similis* from various waters were reanalyzed and the average or modal lengths for each size group were plotted together with the present data (Figure 9). Except for the points derived from the offshore population in the subarctic North Pacific, where the environment is quite different from that of southern California, the majority of cohorts had average or modal lengths which fell within the growth curves of three year classes fitted by eye.

These data indicate the following: 1) as expected from spawning season data, in most cases the modal progressions are evident starting in winter or early spring, 2) growth trends of *S. similis* off southern California appear similar to the population off Oregon (Pearcy and Forss 1969), and 3) growth rates do not vary greatly among many different populations, although there is evidence that a few modal groups grew about twice as rapidly as the ordinary one.

The ratio of females to males in all collections was 1.3:1 (553:422). Sex ratio in a cohort was not skewed greatly towards females until the modal length of the female population reached about 13 mm CL. At that point, the males of the cohort rapidly disappeared from the collection, accounting for the observed imbalance in sex ratio (69:2).

DISCUSSION

Ontogenetic Migration

Omori (1979) found experimentally that: 1) ovigerous females of *S. similis* shed their eggs at night, 2) the eggs took 105 h to hatch into nauplii

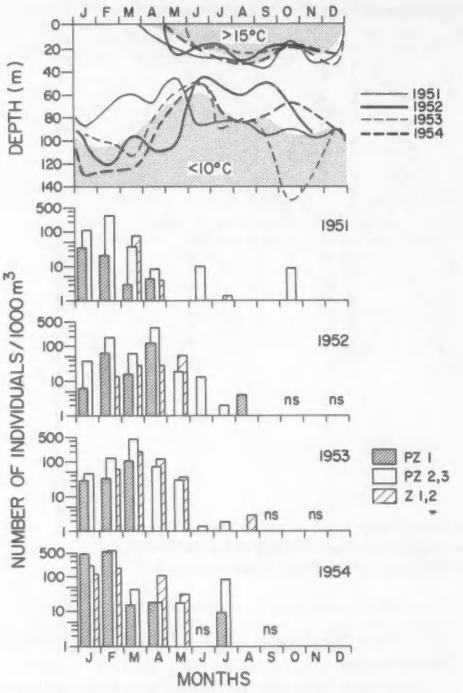

FIGURE 7.—Isotherms of 10° and 15°C and occurrence of larvae of *Sergestes similis* at CalCOFI Stn. 90.37, 1951-54, off southern California at 0-140 m. Shadow indicates zones where temperatures exceed the average 10°-15°C range of 1950-55. No sampling indicated by ns. PZ, protozoeal stages; Z, zoeal stages.

at 10°C, and 3) mortality increased greatly in temperatures beyond 10°-15°C. We do not know the depth where spawning and hatching of *S. similis* take place in the natural habitat. However, the laboratory observations, coupled with biological information on the other species of sergestids and euphausiids (Omori et al.[7]), indicate that the eggs of *S. similis* are shed in shallow water at night when ovigerous females rise upwards. Adult *S. similis* seldom occur above the 50-m level at night where the temperature is usually >13°C off southern California. Assuming that

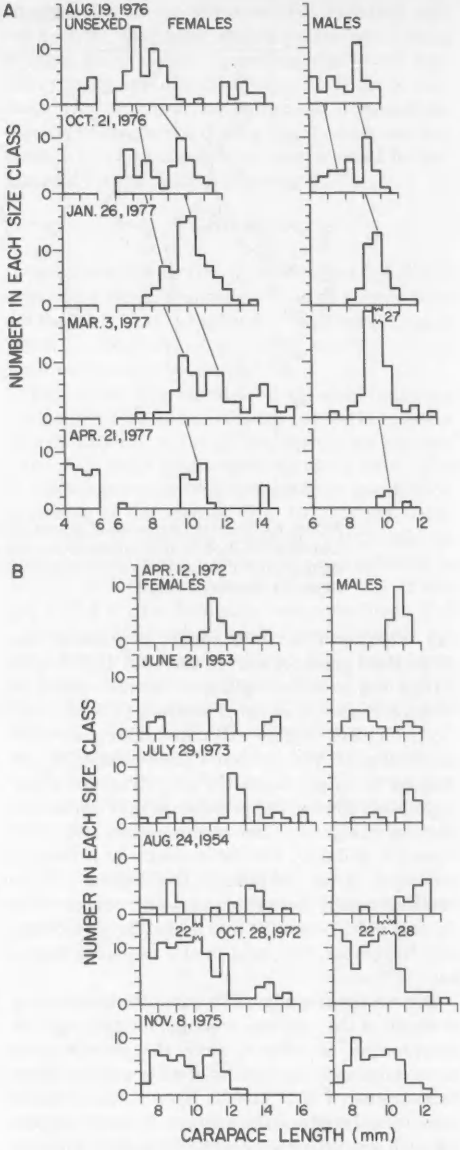

FIGURE 8.—Length-frequency histograms of *Sergestes similis* collected with a 6-ft IKMT (A) and a 10-ft IKMT (B) off southern California. The samples were arranged in monthly order regardless of the year of sampling. Lines trace development of significant cohorts.

[7]Omori, M., M. Mutoh, and M. Kaetsu. 1974. Prediction of *Sergia lucens* fishery in 1974/75 season. [In Jpn.] Unpubl. manuscr., 5 p., distributed at the annual meeting of the "Sakura-ebi" Fishing Unions, Shizuoka Prefecture, Japan.

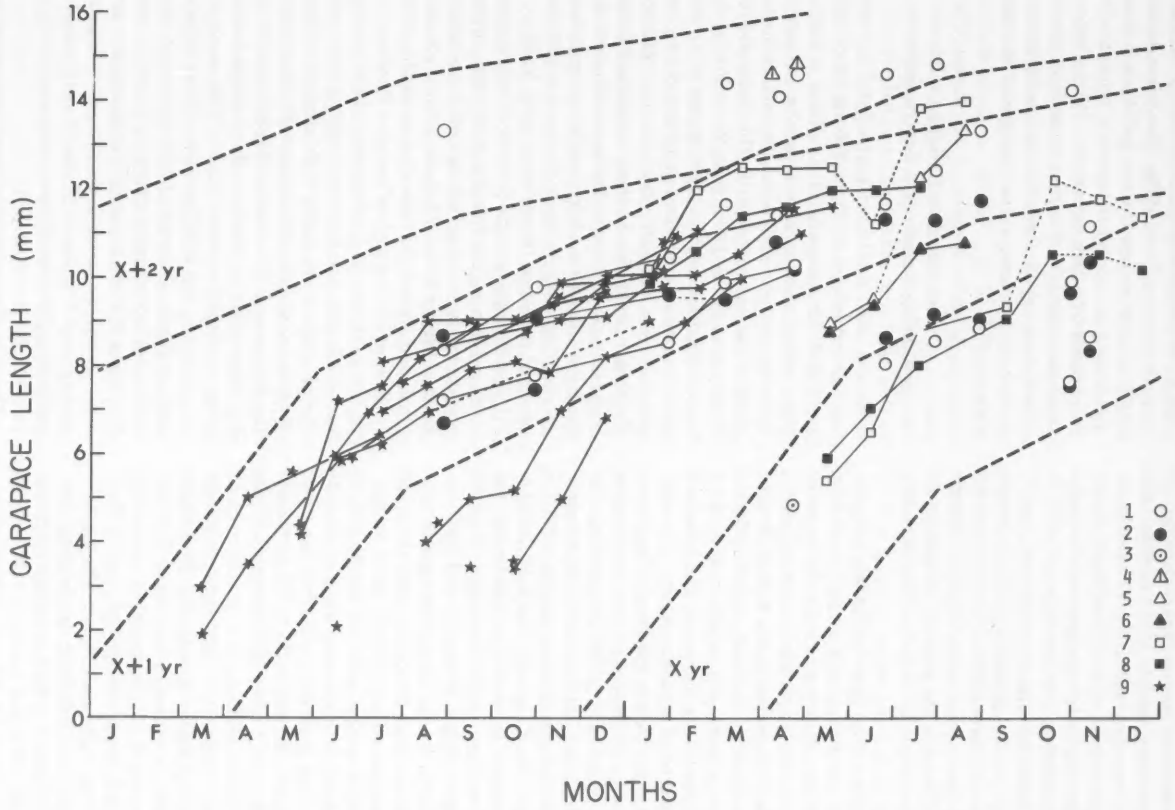

FIGURE 9.—Growth trends in different waters of *Sergestes similis*, derived from average modal length of different cohorts. Solid and dashed lines trace development of cohorts. Solid lines trace sequences considered clear, dashed trace those less clear. Data sources: 1, present study, female; 2, the same, male; 3, the same, unsexed juvenile; 4, off Japan, female (Mutoh and Omori 1978); 5, subarctic North Pacific, female (Omori et al. 1972); 6, the same, male; 7, off southern California, female (Genthe 1969); 8, the same, male; 9, off Oregon, sexes combined (Pearcy and Forss 1969).

spawning takes place around 50 m and using data on both the sinking velocity of the eggs and the development time of eggs at 10°C, we can estimate that the eggs sink to about 220-m depth before hatching. The ambient temperatures which eggs may encounter during their descent are 7°-13°C. It is probable that some eggs are laid deeper than 50 m. However, like the population off the Oregon coast (Pearcy and Forss 1969), *S. similis* is seldom distributed over the continental shelf off southern California. Therefore the majority of eggs would not sink to the bottom but remain within the water column.

A comparison of vertical distribution patterns at all stations confirms the following hypotheses: 1) the occurrence of larvae is restricted to water <140 m where the temperature range is 9°-16°C, 2) the larvae often appear in the 0-20 m level at night but rarely in the daytime, and 3) the larval distribution is more restricted inshore than offshore to a limited vertical range. The descent of eggs and ascent of naupliar larvae are well documented in the oceanic euphausiid *Euphausia superba* and *Meganyctiphanes norvegica* (Mauchline and Fisher 1969). Presumably the nauplii of *S. similis* rise from 200 m or deeper to layers where the temperature is usually >10°C. In this manner, the nauplius, which is probably highly vulnerable to predation, develops in the less hazardous layers which are deeper than the following larval stages. Protozoeal and zoeal larvae stay mostly in the shallower environment which is relatively rich in food (phytoplankton and microzooplankton). They perform daily vertical migration starting PZ1, and their downward migration at daytime becomes more marked with each stage. This hypothesis is further supported by the positive phototaxis in N3 to PZ1 larvae and negative phototaxis after PZ2 observed in the laboratory (Omori 1979).

According to Omori (1974), the larvae of pelagic shrimps can be classified into several types on the basis of their ontogenetic migration. The first group is composed of the species living in the epipelagic and upper mesopelagic zones. Their larvae perform migration within the euphotic zone. *Sergestes similis* belongs to this group, having a similar pattern to that described for *Sergia lucens* (Omori 1974), but the negatively buoyant eggs of *Sergestes similis* differ from *Sergia lucens* eggs which have density similar to seawater.

Adult *Sergestes similis* were abundant inshore off Oregon during the winter, but they tended to shift to an offshore distribution during the summer (Pearcy and Forss 1969). This inverse relationship between nearshore and offshore stations indicates a horizontal ontogenetic migration of this species by active swimming with the help of subsurface currents. The movement by a species to nearshore regions for spawning is a characteristic behavior among several sergestid shrimps (Omori 1974).

Relationship Between Spawning Season and Environment

Larvae of *S. similis*, in particular PZ1, were more abundant inshore than offshore, which indicates that the spawning of *S. similis* is taking place mainly close to shore above the continental slope off southern California (but not as far inshore as the continental shelf). The assumption by Pearcy and Forss (1969) that *S. similis* in the Oregon population spawns during most of the year with a seasonal minimum occurring during the summer was partially true in the southern California population as there were small pulses of spawning in summer and autumn. However, the southern California adult population appears to be recruited largely from the local population spawned from late December to early April.

One may argue that the decrease of larvae in the study area in summer and autumn was caused merely by the seasonal change off the southern California gyre. It would be interesting to compare our data with samples from stations outside of the northward flowing path of the gyre. However, we do not think that such an extreme absence of larvae in summer and autumn is taking place with the year-round spawning of *S. similis*. At least some larvae should have successfully remained in the study area to yield noticeable recruitment during those months. Incidentally, females having fully developed ovaries (Omori 1979) were seldom found in the IMKT collection from summer and autumn. Genthe (1969) assumed that maximum reproductive activity of *S. similis* from the Santa Barbara Channel was in summer and autumn, but his assertion that juveniles collected in August of 5.0-6.5 mm CL are 11 or 12 mo old is misleading. Shrimp of this size are more likely to be of the 6-7 mo class.

Omori et al. (see footnote 7) studied the relationship between environments and reproductive behavior of another sergestid, *Sergia lucens*, in Suruga Bay, Japan, and found that the com-

mencement of spawning and the survivorship of larvae are closely related to the ambient temperature rather than the quantity of food available. This study showed that: 1) *S. lucens* started spawning in June, immediately after the temperature exceeded 18°C at 20-50 m, and the number of larvae increased with increasing vertical thickness of the optimum temperature zone for the growth of larvae (18°-25°C), 2) the population size of *S. lucens* was determined by the abundance of larvae during the first half of the breeding season, June-August, and 3) the abundance of larvae was often related to the fluctuation in vertical width of the optimum temperature zone. During midsummer the warming of surface waters above to 25°C and the shoaling of cold water <18°C restricted the optimum temperature zone, and consequently the mortality of protozoeal larvae increased.

As with *S. lucens*, a rise in temperature may trigger the commencement of spawning of the *Sergestes similis* population in the northern subarctic waters where surface temperature is <10°C during most of the year. However, this seems not to be the case for the southern California population where favorable temperatures were available year-round in some stations between 50 and 100 m. Yet, the spawning began abruptly when the temperature around 100-m depth began to rise. Abundance of larvae was greatest during the period when the vertical thickness of the optimum temperature zone was the greatest, and spawning activity almost ceased both when the ambient temperature was lowered by coastal upwelling and when warm surface water subsequently appeared. Thus, the spawning season of *S. similis* is not always positively correlated with the upwelling which causes environmental enrichment and subsequent increase of plankton biomass in the southern California eddy. The correlation of spawning to coastal upwelling in *Euphausia pacifica*, another very abundant species of the California Current zooplankton assemblage, is the most striking difference affecting the spawning seasons of that organism and *S. similis*. Similar to *S. similis*, the southern California population of *E. pacifica* seems to be adapted for larval development between 12° and 16°C, but its spawning is highest when coastal upwelling is strongest in May-June (Brinton 1976). Although true mechanisms remain unexplained, we theorize that the distinctive spawning season of *S. similis* in southern California is based mainly on the adaptation of this species to the vertical thickness of optimum temperature. The vertical thickness of the optimum temperature zone was also correlated with the abundance and survival of larvae of *S. similis*. The cumulative depths of the optimum temperature ranges for *S. similis* from January to March were 220, 318, 311, and 380 m from 1951 to 1954 whereas the average numbers of protozeal larvae occurring from January to April were 129, 218, 224, and 543 individuals/1,000 m^3, respectively. In 1951, zoeal larvae were found in the lowest numbers when the cumulative depth was the smallest.

One possible interpretation of the irregular small pulse of spawning of *S. similis* in seasons other than winter and early spring is that shrimp which reproduce during these periods are carried from northern offshore waters, i.e.,subarctic North Pacific, to the study area. If temperatures of 9°-10°C in the habitat of *S. similis* really trigger the commencement of spawning, those living in subarctic waters would start spawning later than July in most areas. The yearly mean velocity of the eastward component of the North Pacific Drift is about 3 cm/s at the surface in the areas lat. 45°N west of long. 150°W. On the other hand, a strong south-flowing current, which flows at the velocity of 5-10 cm/s but occasionally >20-30 cm/s is observed throughout the year both at the surface and at 200-m depth off the west coast of the United States (Wyllie 1966; Stidd[8]). If part of the population of *S. similis* near lat. 47°N, long. 140°W, e.g., where tremendous numbers are eaten by baleen whales (Omori et al. 1972), is carried southeastward by the currents, the shrimp can easily reach the southern California coast within 2 yr at a mean speed of 5 cm/s of flow. The spawning occurs in the summer off California due to continuous recruitment of such northern populations. An electrophoretic study of *S. similis* population may help to answer this question, although, due to diverse trophic regimes, genetic variability of the southern California population may be too large to distinguish it from the subarctic population (see Valentine and Ayala 1976).

Another possible interpretation is that the phenomenon is caused by the adaptation of the local population to mid latitude irregularities in oceanographic and trophic conditions. It has been observed for several penaeids, sergestids, and euphausiids in temperate and tropical regions

[8]Stidd, C. K. 1974. Ship drift components: means and standard deviations. SIO Ref. 74-33, 57 p.

that the ovary may contain ova at different developmental stages and that not all ova are necessarily released at once (King 1948; Mauchline 1968; Roger 1973; Omori 1974). We observed that *S. similis* off southern California always retained considerable numbers of immature ova after spawning. Because the volume of a pair of mature ovaries from this shrimp represents about 10% of the body volume, we can estimate from the volume of each egg that one female has at least 1,500 but probably closer to 2,000-2,500 eggs. Nevertheless, the number of eggs released by a female in the laboratory was always <1,140 (Omori 1979). Thus, as has been pointed out for *Euphausia pacifica* off southern California (Brinton 1976), it appears possible that under optimal environmental conditions small ova of *S. similis* may develop later and produce a second spawning. If a female, which produced the first clutch in late December, released the second clutch 3-4 mo later, two modal size-groups might be seen sometimes in the same age-group. It is probable that unfavorable environmental conditions would prevent the spent ovary from maturing again until the following year. Further evidence of this phenomenon is provided by the increase in the number of spent females and the decrease in the number of fully grown ova in ovaries of *S. similis* off southern California and Oregon during the summer (Genthe 1969; Pearcy and Forss 1969). The length-frequency histograms in October 1972, November 1975, and from August 1976 to March 1977 (Figure 8) indicate either the occurrence of multiple spawnings for *S. similis* or individuals from farther north being mixed into the southern California population.

Growth, Sexual Maturity, and Longevity

If *S. similis* population is composed of 0 age-group shrimp only and all attain sexual maturity after about 1 yr, the size structure of the population sampled shows the presence of only one or two size groups. However, the obvious occurrence of three size groups of females during certain periods of the year in this study indicates that the females of *S. similis* live 2 yr or more. Large females, 13-16 mm CL, carrying developed ovaries are sometimes collected, indicating that *S. similis* can reproduce at least twice during its lifetime. The absence of male individuals >14 mm CL resulted in a strong imbalance of sex ratio, indicating that the males die out at an age of <20 mo. Genthe (1969) showed evidence of sex reversal (protandrous hermaphroditism) from male to female in *S. similis*. Similar phenomena have been observed in other sergestids of the genus *Acetes* (Omori 1975). A detailed study is needed to determine the meaning of these findings, although at the present time we believe that the variance may be explained by abnormalities, since the frequency of occurrence is small. The bias in sex ratio favoring females above a certain size indicates the possibility of multiple fertilizations by males. Thus some females of the 2 age-group may mate with males of the 1 age-group.

We obtained an average growth trend of *S. similis* throughout its life by shifting the average or modal lengths of populations off the California and Oregon coasts horizontally in accordance with the month of their sampling. The growth of *S. similis* >6 mm CL was best fitted by the von Bertalanffy equation (Figure 10):

$$l_t = 14.7(1 - e^{-0.00378t}) \text{ for females, and}$$
$$l_t = 12.0(1 - e^{-0.00481t}) \text{ for males,}$$

where l_t is the carapace length in millimeters at t days. Because of the large mesh sizes of the IKMT nets, however, any average or modal length calculated from these samples over considerable size ranges on either side of 7 mm CL is probably greater than the length of the natural population. Therefore, the initial modal length of the 3-mo old population was fit by eye and connected with those growth curves of larval and early postlarval stages at 10° and 14°C which were obtained under laboratory conditions. It took 52 days for *S. similis* to reach the first postlarval stage at 14°C (Omori 1979). Under these conditions the logistic equation (Figure 10B) seemed to give the better fit to the growth curves:

$$l_t = \frac{14.7}{1 - e^{-0.00920(t-234.5)}} \quad \text{for females,}$$

$$l_t = \frac{12.0}{1 - e^{-0.01254(t-188.4)}} \quad \text{for males.}$$

Growth is very rapid during the postlarval stages. The juveniles at 4-8 mo old grow, at 0.91 mm CL/mo, during the period from April to August (logistic equation). The biomass of total zooplankton, as well as young *Calanus* and *Euphausia*, which are considered to be the most important food for juvenile and adult *S. similis*,

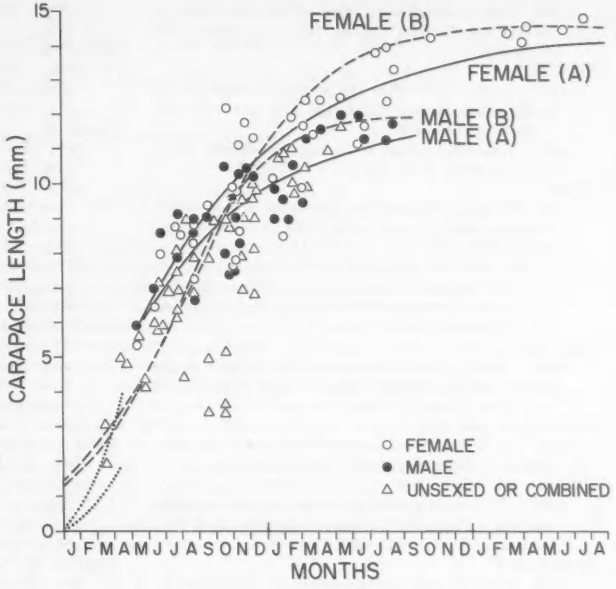

FIGURE 10.—Average growth of *Sergestes similis* off the California and Oregon coasts. Solid lines (A) are growth curves fit by the von Bertalanffy equation and (B) are those fit by the logistic equation. Dashed lines are growth curve of early developmental stages of 10° and 14°C determined in the laboratory (Omori 1979).

usually peaks in the April-July period in southern California waters (Mullin and Brooks 1970; Brinton 1976). Shrimp which encounter the best feeding conditions probably grow rapidly with low mortality rates and form distinctive modal groups such as those traced in Figure 9. The growth rate gradually decreases after 10-mo old, and the females add only 5 mm CL in 20 more months before dying. The difference in growth rates between the sexes becomes apparent after the shrimp attain a length of about 8 mm CL. The males grow slower than the females, but attain sexual maturity ½-1 mo earlier than females because the females become mature at 10.5-11.0 mm CL, whereas the males mature at 9.5-10.0 mm CL (see Genthe 1969; Omori 1979). Since five data points for females on the upper right-hand side of Figure 10 are on the asymptote, it is highly speculative whether these shrimps represent that age-group, or possibly an age-group spawned 5-6 mo later; in which case they would be placed on a different curve. It is apparent, however, that the longevity of the females of *S. similis* is more than 2 yr and that they spawn in two successive spawning seasons during their lives. These observations agree well with those of Matthews and Pinnoi (1973) on *Sergestes arciticus* Kröyer, which is the most closely related species to *S. similis* (Judkins 1972), in Kursfjordan, western Norway.

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THE OCEANIC MIGRATION OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*, ALONG THE ATLANTIC COAST

RICHARD J. NEVES[1] AND LINDA DEPRES[2]

ABSTRACT

The migratory route of American shad, *Alosa sapidissima*, in the Atlantic Ocean was studied using 14 yr of catch data collected during bottom trawl surveys by the U.S. National Marine Fisheries Service (and its predecessor) and cooperating foreign countries. All shad catches occurred at bottom temperatures from 3° to 15°C, with the most frequent catches between 7° and 13°C. Water temperatures between initial and peak entry of shad into home estuaries along the Atlantic coast are within the same thermal regime (3°-15°C). During the summer, all shad catches occurred north of lat. 40°N in two primary areas: Gulf of Maine and an area south of Nantucket Shoals. Previous studies on food habits and differences in time of capture during National Marine Fisheries Service surveys indicated that shad were vertical migrators, probably following the diel movements of large zooplankters in the water column. Shad were generally absent from the Gulf of Maine by late autumn, and concentrations were found between lat. 39° and 41°N during the winter. Based on previous tagging studies, National Marine Fisheries Service surveys, and coastal temperature data, most prespawning adults enter coastal waters along the Middle Atlantic Bight from lat. 36° to 40°N and then proceed north or south to natal rivers. Coastal surveys for river herring by North Carolina's anadromous fishery research program and commercial shad catches reported to the International Commission for the Northwest Atlantic Fisheries by member nations concur with our proposed bottom temperature (3°-15°C)-migratory route hypothesis for shad.

The American shad, *Alosa sapidissima*, is an anadromous fish ranging from the St. Johns River, Fla., to the St. Lawrence River, Canada (Walburg and Nichols 1967). Meristic and tagging studies indicate that discrete spawning populations of shad exist in river systems along the Atlantic coast (Hollis 1948; Hill 1959; Nichols 1960, 1966; Carscadden and Leggett 1975a). Juveniles leave freshwater in autumn and generally remain in the ocean for 3-5 yr before returning to their natal rivers to spawn. Spawning runs occur in a south to north temporal progression, beginning as early as December in Florida and as late as June in Canada (Walburg 1960). Virtually all shad south of Cape Hatteras, N.C., die after spawning, whereas the percentage of repeat spawners in rivers north of North Carolina increases with latitude (Leggett 1969; Chittenden 1975).

A considerable amount of literature exists on this species because of its commercial and recreational importance inshore, but little research has been done on the oceanic phase of its life history. Talbot and Sykes (1958) provided the first evidence of an annual oceanic migration based on 19 yr of tagging studies by the U.S. Fish and Wildlife Service. Tag returns indicated that shad from U.S. rivers congregated with those from Canadian rivers (Vladykov 1950, 1956) in the Gulf of Maine during summer and autumn and moved south to possibly overwinter off the Middle and South Atlantic States (Talbot and Sykes 1958; Walburg 1960; Walburg and Nichols 1967; Cheek 1968). In the spring, shad moved north or south toward natal rivers to spawn.

Temperature monitoring in rivers with major shad runs, and laboratory experiments, have provided convincing evidence that the timing of diadromous movements corresponds with specific water temperatures (Walburg and Nichols 1967; Chittenden 1969, 1972; Williams and Bruger 1972; Leggett and Whitney 1972; Leggett 1973). Leggett and Whitney (1972) also postulated that the oceanic distribution of shad was temperature-controlled; tag returns plotted on surface isotherm charts fell within the 13°-18°C isotherms. However, all of the tag returns used to establish this "migrational corridor" at sea were collected inshore during the spring coastal migration toward

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home rivers. The correlation between offshore distribution and surface temperatures was therefore based on extrapolation.

The U.S. shad fishery is essentially an inshore operation and commercial catch records have limited value in evaluating the distribution of shad at sea. Previous tagging studies have relied on other commercial fisheries for offshore tag returns, but these fisheries concentrate effort at a time or place where principal species aggregate. Tag returns from shad taken as bycatch may therefore contain a geographical bias and reflect only the distribution of fishing effort. This paper examines offshore collections of shad from 14 yr of bottom trawl surveys by United States and foreign research vessels and interprets available literature on the coastal occurrence of shad. An alternative temperature-based hypothesis is presented to explain the offshore migratory cycle of shad.

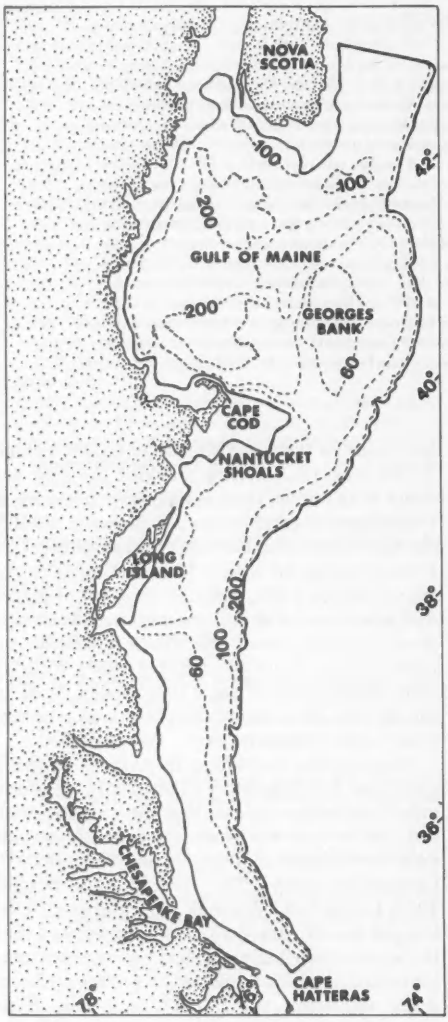

FIGURE 1.—National Marine Fisheries Service bottom trawl survey area between 27 and 366 m, Cape Hatteras, N.C., to Nova Scotia, western North Atlantic.

METHODS

The U.S. National Marine Fisheries Service (NMFS) and its predecessor have conducted autumn bottom trawl surveys since 1963 using the RV *Albatross IV* and the RV *Delaware II*. The survey area extends from Nova Scotia to Cape Hatteras, out to 366 m (200 fm) (Figure 1) and is stratified into geographical zones based on depth and area. Coastal sampling stations are outside the 27-m (15-fm) depth contour. Middle Atlantic stations between New Jersey and Cape Hatteras were added during autumn 1967. A stratified random sampling design is used in the surveys; trawl stations are allocated to strata in proportion to stratum area and randomly assigned within strata (Grosslein 1969). A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner is towed at each station for 30 min at an average speed of 3.5 kn. Autumn surveys were conducted 24 h/day during 1963-76, between 3 September and 16 December.

Spring bottom trawl surveys have been conducted by NMFS since 1968 over the same geographical area (Figure 1). The No. 36 Yankee trawl was used from 1968 to 1972 and a larger No. 41 Yankee trawl from 1973 to 1976. Trawling procedures were the same as during autumn surveys and occurred between 4 March and 16 May. A detailed description of NMFS bottom trawl surveys and survey procedures is provided by Flescher[3] and Grosslein.[4]

In addition to U.S. cruises, periodic autumn trawl surveys were conducted cooperatively with

[3]Flescher, D. 1976. Research vessel cruises, 1963-1975 National Marine Fisheries Service Woods Hole, Massachusetts. NMFS, Woods Hole, Mass., Lab. Ref. No. 76-14, 30 p.

[4]Grosslein, M. D. 1969. Groundfish survey methods. NMFS, Woods Hole, Mass., Lab. Ref. No. 69-2, 34 p.

the U.S.S.R., Poland, and France from 1969 to 1976, mainly between Georges Bank and Cape Hatteras. Spring trawl surveys, intended primarily as juvenile herring surveys, have been made since 1973 by vessels from U.S.S.R., Poland, German Democratic Republic, and Federal Republic of Germany between Nova Scotia and Cape Hatteras. Most of the foreign surveys followed NMFS sampling procedures, sampled all or selected strata within respective survey areas, but used various types of bottom trawls. All spring and autumn surveys and additional cruises during summer and winter are summarized in Table 1. Survey station and catch data pertinent to this study included: date, location, time, depth, bottom and surface temperatures, and number, length frequencies, and weight of shad caught.

We plotted catch locations from all surveys (Table 1) by 10′ rectangles of latitude and longitude on depth contour maps according to month or season. Locations of shad collections during spring (March-May) and autumn (September-November) were plotted by month. Summer (June-August) and winter (December-February) surveys were grouped by season because of less sampling effort and lower catch frequency. Commercial shad catches by month reported to the International Commission for the Northwest Atlantic Fisheries (ICNAF) by member nations from 1970 to 1975 were provided by Hodder[5] and used to define major shad catches within each ICNAF division and their correlation with distribution patterns based on survey data. Surface and bottom temperatures (nearest 1°C) were plotted for each trawl tow that collected shad; foreign catches with missing temperature data were omitted from this analysis. Additional oceanographic data on temperature (Walford and Wicklund 1968; Colton and Stoddard 1972; Churgin and Halminski 1974; U.S. Coast Guard Oceanographic Unit[6]) and oceanic currents (Bumpus and Lauzier 1965; Stommel 1965; Bumpus 1973) were reviewed for seasonal patterns along the Atlantic coast.

RESULTS

Bottom trawls at 10,435 stations during the 77 surveys collected 4,770 subadult and adult shad at 527 stations throughout the survey area. United States and foreign research vessels accounted for 315 and 212 of the successful collecting stations, respectively. Shad ranged in size from 8 to 50 cm fork length (FL). Surface and bottom temperatures were recorded at 448 of these stations and used to plot catch frequency at 1°C intervals. Shad were collected at survey stations with surface temperatures between 2° and 23°C, and frequent catches occurred throughout most of this temperature range (Figure 2). Bottom temperatures at successful collecting stations ranged from 3° to 15°C, but primarily between 5° and 13°C (Figure 3). Most stations with bottom temperatures <3°C occurred in the Gulf of Maine during late winter and early spring; stations with bottom temperatures >15°C were mainly off the mid-Atlantic coast during late summer and early autumn. This apparent relationship between shad occurrence and bottom temperatures was examined further by comparing the catches of shad with total sampling effort at each temperature (Table 2). Bottom temperatures during surveys ranged from 1° to 23°C, but shad were captured only between 3° and 15°C. Shad catches occurred more frequently at

TABLE 1.—Summary of bottom trawl surveys conducted by United States and foreign research vessels between Cape Hatteras, N.C., and Nova Scotia, 1963-76.

Season	Country	No. of surveys	No. of stations	Inclusive dates
Spring	United States	15	2,514	4 Mar.-16 May
	Foreign	10	597	26 Feb.-29 May
Summer	United States	4	810	7 July-28 Aug.
	Foreign	6	618	9 Aug.-3 Sept.
Autumn	United States	21	3,657	3 Sept.-16 Dec.
	Foreign	18	1,676	3 Sept.-11 Dec.
Winter	United States	3	563	16 Jan.-8 Apr.
Totals		77	10,435	

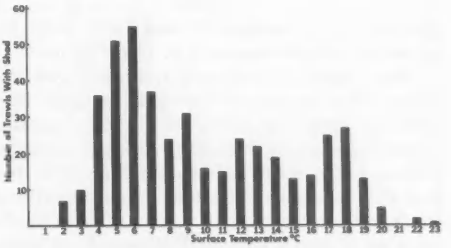

FIGURE 2.—Surface temperatures at 448 stations where American shad were collected during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

[5]V. M. Hodder, ICNAF Office, Dartmouth, N. S., Canada B2Y 3Y9, pers. commun. July 1977.

[6]U.S. Coast Guard Oceanographic Unit. 1970, 1975. Monthly temperature charts, January to December 1970, January to December 1975, available U.S. Coast Guard Oceanographic Unit, Bldg. 159-E Navy Yard Annex, Washington, DC 20590.

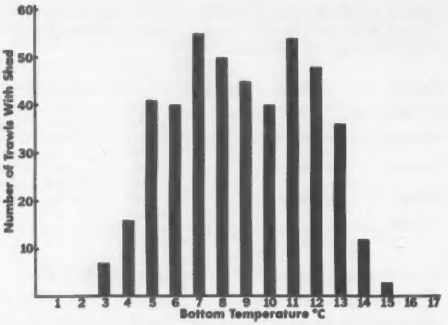

FIGURE 3.—Bottom temperatures at 448 stations where American shad were collected during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

TABLE 2.—Total sampling effort, number of shad catches, and percent catch frequency of shad at each bottom temperature during bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

Bottom temperature (°C)	Total no. of trawls	Trawls with shad	
		No.	%
1	16	0	0
2	104	0	0
3	270	7	2.59
4	567	16	2.82
5	987	41	4.15
6	964	40	4.15
7	1,047	55	5.25
8	997	50	5.02
9	909	45	4.95
10	750	40	5.33
11	741	54	7.29
12	739	48	6.50
13	626	37	5.91
14	333	12	3.60
15	164	3	1.83
16	71	0	0
17	56	0	0
18	41	0	0
19	30	0	0
20	[illegible]	0	0
21	34	0	0
22	19	0	0
23	5	0	0

temperatures between 7° and 13°C, with the greatest capture frequency at 11°C (Table 2).

Ocean depths at stations with shad ranged from 20 to 340 m, but most of these stations (65%) were <100 m deep (Figure 4). Of the 527 successful collecting stations, 269 (51%) occurred at depths between 50 and 100 m. Since trawling effort during U.S. spring and fall surveys was proportional to the area of each depth interval (Table 3), the number of shad catches within these depth strata was amenable to chi-square analysis. A comparison between shad catches at each depth interval and catches at all other depths combined indicated

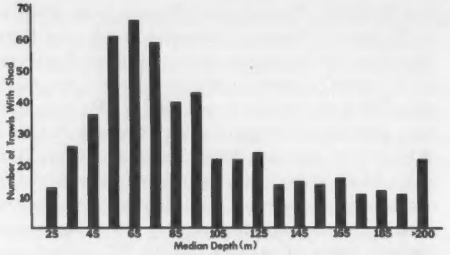

FIGURE 4.—Frequency of American shad catches with depth at 527 survey stations, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

TABLE 3.—Depth intervals within the survey area and associated shad catches during U.S. bottom trawl surveys, 1967-76, Cape Hatteras, N.C., to Nova Scotia.

Depth interval (m)	Survey area		Number of trawls with shad		
	km²	%	Observed	Expected	χ^2
27-55	47,412	25.4	45	58	3.89*
56-110	55,009	29.5	109	68	35.10**
111-185	53,789	28.9	53	67	4.13*
186-366	30,181	16.2	23	37	6.32*
Totals	186,391	100.0	230	230	

*$P<0.05$.
**$P<0.01$.

that the greater capture frequency in the 56-110 m interval was highly significant ($P<0.01$); shad catches at all other depths were significantly fewer ($P<0.05$) than expected (Table 3).

Spring surveys were conducted mainly in March and April, accounting in part for the more frequent collections during these 2 mo (Figure 5). In March, shad were distributed along the Middle Atlantic Bight. Most fish between Long Island, N.Y., and Cape Cod, Mass., were taken in 60-200 m of water, many along the outer continental shelf (Figure 5). Few shad occurred in <60 m of water north of lat. 40°N, whereas most catches south of Long Island were at depths <60 m.

During the summer, shad were not captured south of lat. 40°N (Figure 6). Forty-six collections in July and August were made in two general areas: the Gulf of Maine and southeast of Cape Cod, near Nantucket Shoals. Mean depth at these stations was 95 m, but ranged from 35 to 214 m. Catches were distributed along the coastal margin of the Gulf of Maine and the southern half of Georges Bank; most trawling stations in the deeper, central Gulf did not collect shad.

October received the greatest trawling effort during autumn surveys. Shad were again distrib-

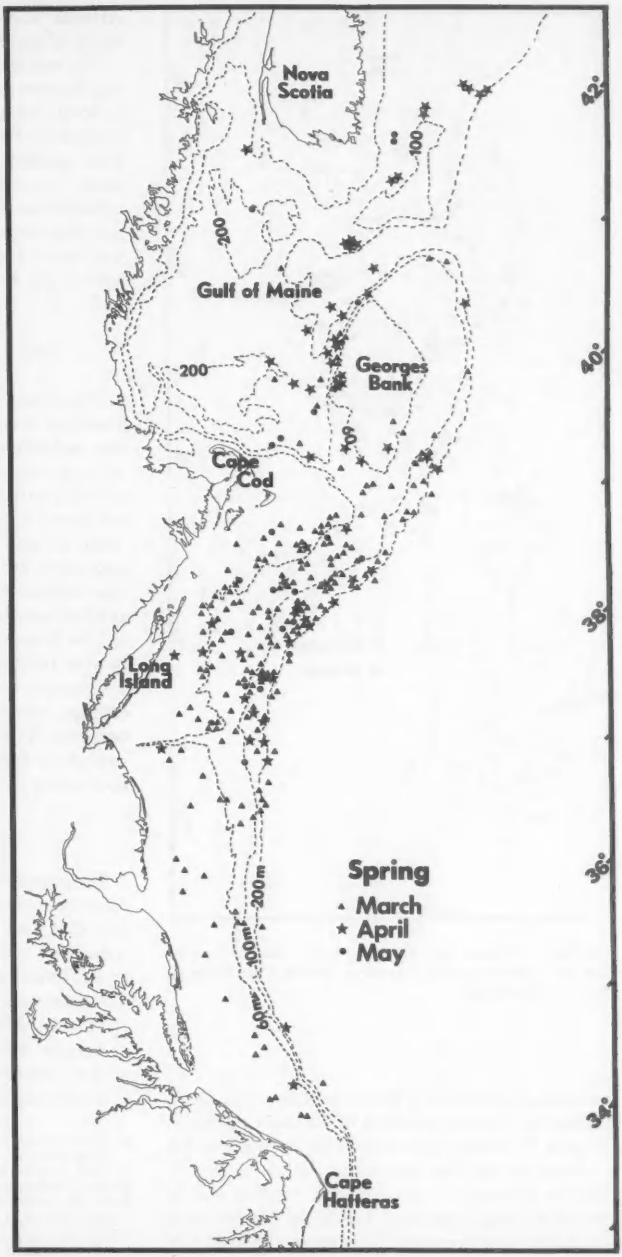

FIGURE 5.—Location of all American shad catches during spring bottom trawl surveys, 1968-76, Cape Hatteras, N.C., to Nova Scotia.

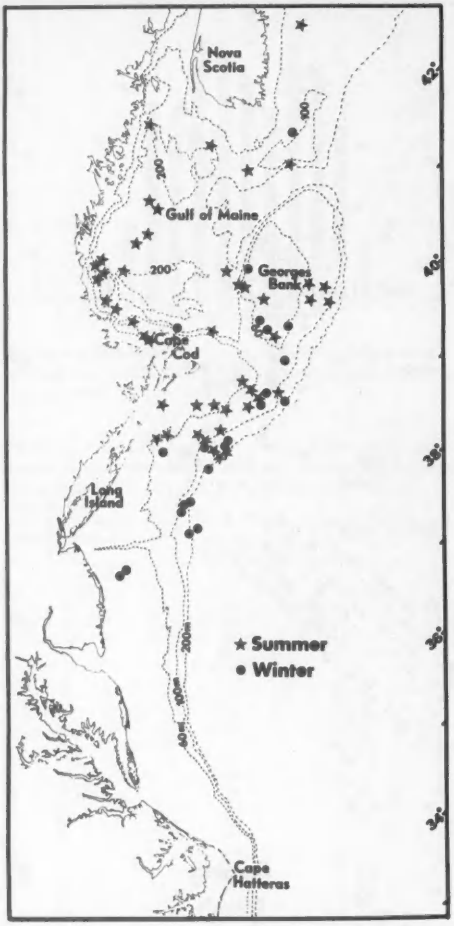

FIGURE 6.—Location of all American shad catches during summer and winter bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

uted along the Gulf of Maine and Georges Bank perimeter, as well as south of Nantucket Shoals (Figure 7). Most of these captures were along the continental shelf at depths of >60 m. Monthly catches indicated a southward movement out of the Gulf of Maine in late autumn, although some shad remained there into November. During 10 yr of autumn bottom trawl surveys along the Middle Atlantic States, shad were never collected offshore south of lat. 39°N.

The relatively low number of successful trawling stations during the winter may be inadequate to define the southern limit of the wintering area (Figure 6). Winter catches occurred at 22 stations from southern Long Island (lat. 39°N) to the southern edge of Georges Bank (lat. 41°N) and reflected the same general area where shad began congregating in autumn (Figure 7). Except for two shallow-water stations, winter collections of shad were made at a mean depth of 108 m.

DISTRIBUTION OF INTERNATIONAL CATCHES

The season for major shad catches in ICNAF divisions (Figure 8) agreed closely with distribution according to bottom trawl surveys. Largest annual catches were reported by the United States in Subarea 6 (1,517-2,812 t). United States catches between 1970 and 1976 occurred primarily in Division 6B and ranged from 112 to 1,272 t in March and April. Most of this spring catch was taken by the inshore commercial fishery. The only other catch of comparable size was made in Division 5Ze by the Federal Republic of Germany during September 1973 and totaled 302 t. Catches in Subarea 5 occurred mainly in autumn; however, winter catches were reported in Division 5Zw and 6A between New Jersey and Cape Cod. Canadian catches in Subarea 4 were greatest in May, with decreasing catches throughout the summer.

DISCUSSION

The sampling design of NMFS bottom trawl surveys covers a large area in a relatively short period of time and provides good data on fish distribution and concurrent environmental conditions. Even though these surveys were initially designed to sample primarily demersal species, results do reflect major changes in the abundance of pelagic species as well (Schumacher and Anthony[7]; Anderson[8]). Bottom trawls used during U.S. surveys are less effective on *Alosa* spp. than

[7]Schumacher, A., and V. C. Anthony. 1972. Georges Bank (ICNAF Division 5Z and Subarea 6) herring assessment. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1972, Res. Doc. No. 24, Serial No. 2715, 36 p.

[8]Anderson, E. D. 1973. Assessment of Atlantic mackerel in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1973, Res. Doc. No. 14, Serial No. 2916, 37 p.

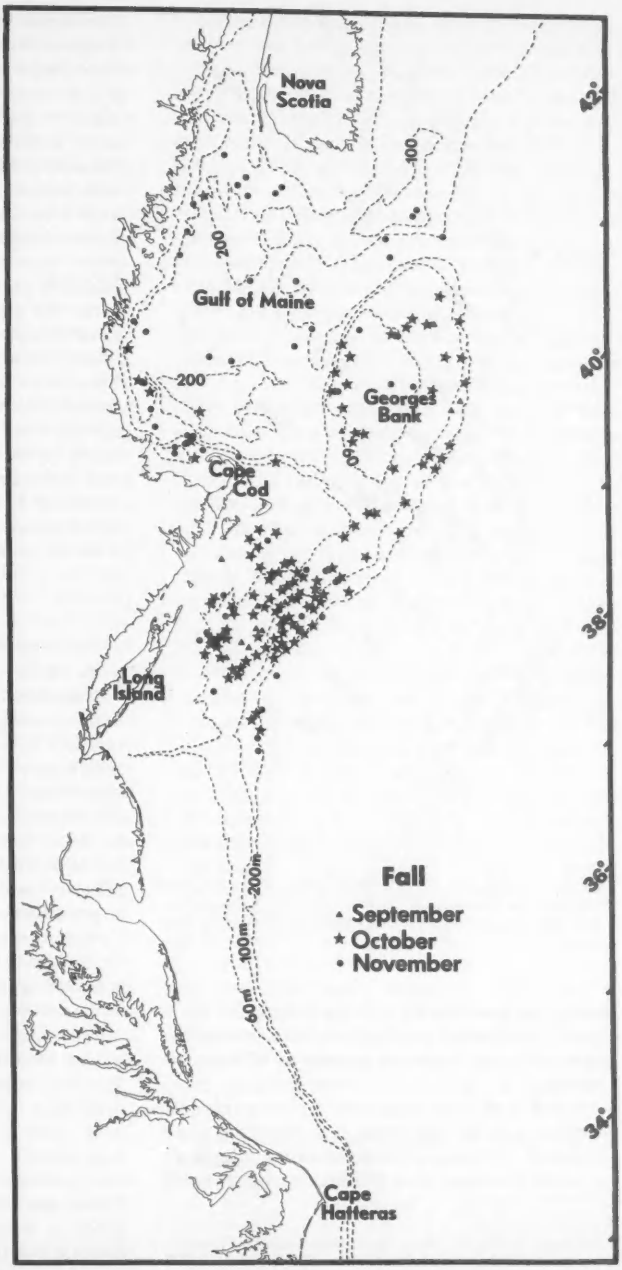

FIGURE 7.—Location of all American shad catches during autumn bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

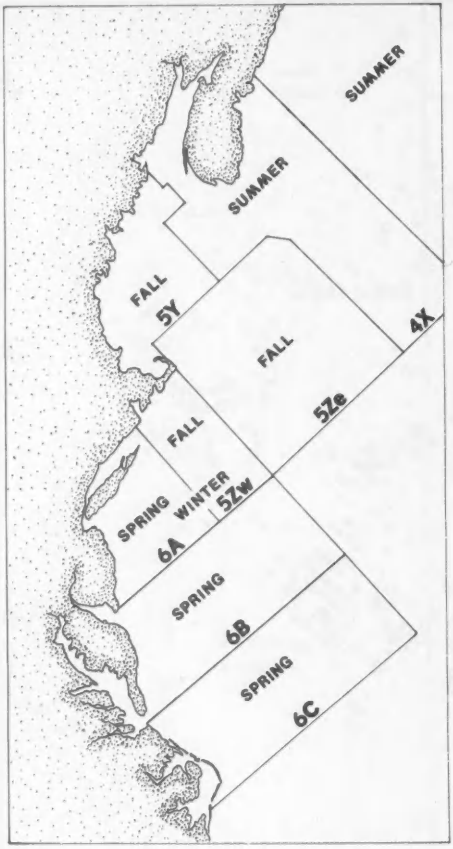

FIGURE 8.—Seasonal distribution of major American shad catches in the International Commission for the Northwest Atlantic Fisheries divisions, 1970-75, Cape Hatteras, N.C., to Nova Scotia.

foreign midwater trawls or the wing trawl (Holland[9]), but bottom trawl survey data provide the most complete, available records on offshore occurrence.

Based on the data presented, survey-related observations to be discussed, and literature to be reviewed, we propose the following migratory cycle for American shad. Offshore movements are limited to areas and depths with near-bottom temperatures between 3° and 15°C. Shad occur most frequently in offshore areas of intermediate depths (approximately 50-100 m). Adults that survive spawning together with subadults migrate to the Gulf of Maine or to an area south of Nantucket Shoals and remain there through the summer and early autumn. During this period of active feeding, shad are vertical migrators and follow the diel movements of zooplankton in the water column. Most shad move out of the Gulf of Maine in autumn with declining water temperatures and congregate offshore, between southern Long Island and Nantucket shoals (lat. 39°-41°N) during the winter. Adults enter coastal waters in a broad front toward the Middle Atlantic coast, as far south as North Carolina during the winter and spring. Shad populations returning to South Atlantic rivers migrate south adjacent to the coast and within the 15°C isotherm to reach home rivers by winter and early spring. North Atlantic populations proceed north up the coast in the spring with the warming of coastal waters above 3°C.

Offshore Distribution

The wide range of surface temperatures at stations where shad were caught does not support the extrapolation of the inshore temperatures-shad migration regime proposed by Leggett and Whitney (1972) to explain offshore movements. The influence of temperature on fish behavior and physiology is most pronounced during the spawning season (Laevastu and Hela 1970), particularly for anadromous fishes. Tag returns within the 13°-18°C isotherms (Leggett and Whitney 1972) may have reflected inshore physiological changes in prespawning adults, leading to higher optimal temperatures approaching those for spawning. Our results indicate that near-bottom temperatures between 3° and 15°C provide a better basis for predicting shad movements in offshore waters.

Offshore catches during NMFS surveys revealed that shad are not limited to the Gulf of Maine in summer months as reported by Talbot and Sykes (1958). Shad were also collected in an area south of Nantucket Shoals during summer and autumn surveys. Although shad from most river systems have been collected in the Gulf of Maine during the summer (Talbot and Sykes 1958), it is not known whether all populations migrate together at sea. Distribution during the spring is widespread and not indicative of a syn-

[9]Holland, B. F., Jr. 1975. Anadromous fisheries research program, northern coastal area. Section II. N.C. Proj. AFCS 11-1 Job 6, 43 p.

chronous species migration as suggested by Leggett (1977). Coastal tagging studies during the spring reveal an aggregation of many spawning stocks that often detour into estuaries along the coast (Sykes and Talbot 1958; Talbot and Sykes 1958; Chittenden 1974; Leggett 1977; White et al.[10]). However, the length of time each population has been inshore is unknown. Until stock identification at sea is feasible, the regional composition and extent of offshore mixing cannot be documented.

The location of winter collections (lat. 39°-41°N) coincides with two previously published capture records (Talbot and Sykes 1958; Walburg and Nichols 1967), but the extent of overwintering in deep water off the continental shelf is unknown. Shad collections in the northern Gulf of Maine during November and December were made at depths >100 m and do not conform (based on previous studies) with the expected migration south in late autumn. These and other shad captured in deep water near Nova Scotia during March (Vladykov 1936) are outside the apparent wintering area, south of Nantucket Shoals. The possibility that some shad overwinter or become thermally isolated in deepwater areas off Nova Scotia (Vladykov 1936; Hodder 1966) needs further investigation.

Circulation patterns along the Atlantic coast do not account for the seasonal distribution of shad according to survey data or their coastal migration routes based on tagging studies (Talbot and Sykes 1958; Leggett 1977). Bottom drift toward shore and coastal drift south in the Middle Atlantic Bight during winter (Bumpus 1973) would aid migrants moving south, but seasonal shifts in directional flow along the east coast and their effect on shad movements are liable to subjective interpretation. Spawning populations moving north and south concurrently could be helped or hindered by circulation patterns in the mid-Atlantic area. We believe that seasonal shifts in isotherms, as influenced by circulation patterns, are of greater importance in defining the migratory route of shad.

Vertical Distribution

Presently there is little information on the depths preferred by shad at sea. We inferred distribution in the water column from three separate sources: food habits, diel differences in catchability, and effectiveness of various trawls in capturing shad. Adult shad are zooplankton feeders and consume primarily large copepods, mysids, and euphausiids (Bigelow and Schroeder 1953; Hildebrand 1963; Leim and Scott 1966). The consumption of food organisms such as mysids and zoobenthos indicates that part of a shad's life is spent near the ocean bottom (Leim 1924; Walburg and Nichols 1967). In general, stomach analyses reveal that shad feed at all depths but particularly where concentrations of zooplankton occur.

Trawling stations where shad were collected during U.S. surveys (24 h/day) were partitioned by capture time (Eastern Standard Time) into day (0600-1800 h) and night (1800-0600 h). Chi-square analysis on time of capture revealed that daytime catches occurred significantly more often ($P<0.01$) than night collections (Table 4). Of the night catches, 25% occurred within 1 h of the daytime interval. Shad were apparently closer to the bottom during daylight hours and thus more susceptible to bottom trawling gear. Further corroboration of this daytime occurrence nearer to the bottom is evidenced by the frequency of shad catches in foreign bottom trawls. During daylight hours in March 1974-76, foreign research vessels used herring trawls to sample 280 stations from Long Island to Georges Bank and recorded shad at 71 (25%) of these stations. Contemporary surveys by the United States in the same area with the No. 41 Yankee trawl sampled 207 daytime stations and collected shad at 22 (11%) of them. Maximum headrope distance off the bottom for the U.S. trawl was 5 m. The larger foreign trawls had a higher opening (6 m) which increased their effectiveness on off-bottom species, although extra-trawl factors such as vessel size, speed, and gear rigging certainly contributed to the greater overall fishing power of these trawls (Grosslein 1969, 1971).

We deduce from the above observations that shad are vertical migrators like other schooling planktivores such as herring, *Clupea harengus*, and mackerel, *Scomber scombrus* (Blaxter 1975;

TABLE 4.—Chi-square test comparing the number of day and night catches of shad during U.S. bottom trawl surveys, 1963-76, Cape Hatteras, N.C., to Nova Scotia.

Time	Observed	Expected	χ^2
Day (0600-1800 h)	217	157.5	
Night (1800-0600 h)	98	157.5	45.0**
Totals	315	315.0	

**$P<0.01$.

[10]White, R. L., J. T. Lane, and P. E. Hamer. 1969. Population and migration study of major anadromous fish. N.J. Div. Fish Game Misc. Rep. No. 3M, 21 p.

Isakov[11]; Rikhter[12]), following the diel movements of zooplankton in the water column. This reliance on zooplankton for food may be an additional factor influencing shad distribution during the year. Zooplankton distribution in the Gulf of Maine during summer and autumn is closely tied to local and regional hydrography (Redfield 1941; Sherman 1966; Cohen[13]); concentrations generally occur along areas of current convergence and divergence (Zinkevich 1967) and at depths <100 m (Bigelow 1926; Whiteley 1948). During winter, the waters around Georges Bank are nearly devoid of zooplankton, whereas sizeable neritic populations occur from Nantucket Shoals to southern Long Island (Clarke 1940; Grice and Hart 1962; Zinkevich 1967). Sette (1950) concluded that water temperature had a limiting rather than causal influence on the seasonal movements of mackerel, and Redfield (1941) noted a parallelism between mackerel distribution and areas of zooplankton abundance. Similarly, Zinkevich (1967) related herring movements to water temperature and seasonal shifts in zooplankton concentrations. Catches of shad during bottom trawl surveys along Georges Bank, Gulf of Maine perimeter, and south of Nantucket Shoals may therefore be related to zooplankton abundance in these areas, but direct evidence is lacking.

Coastal Migration

Tagging studies and the location of NMFS and ICNAF catches during the spring indicate that most shad populations move toward the mid-Atlantic coast from offshore waters, between lat. 36° and 40°N in the winter and early spring. The time and location of tag returns by the mid-Atlantic shad fishery demonstrate that shad from most populations occur in this region during the spring (Talbot 1954; Talbot and Sykes 1958; Leggett 1977; White et al. see footnote 10). Shad tagged near southern Long Island in early spring were recaptured on spawning runs as far south as North Carolina (Talbot and Sykes 1958). Tagging of shad in North Atlantic rivers during the spawning period produced recaptures as far south as the North Carolina coast in subsequent years (Talbot 1954; Vladykov 1956; Talbot and Sykes 1958; Leggett 1977). These tag returns provide an approximate geographical range of entry into coastal waters by returning oceanic migrants (lat. 36°-40°N).

Assuming that the 3° and 15°C isotherms define the northern and southern limits respectively of shad movements at sea, prespawning adults returning to coastal waters from the ocean would face a thermal barrier south of Cape Hatteras. Offshore bottom temperatures along the South Atlantic coast remain above 17.5°C during the year, whereas bottom temperatures on the continental shelf north of Cape Hatteras and inshore temperatures for the South Atlantic coast drop below 15°C by December (Figure 9). The proximity of the Gulf Stream to North Carolina creates a narrow coastal corridor at Cape Hatteras, providing the only migratory route to southern rivers if shad returning to these home rivers are to remain within their marine temperature regime. Migration toward shore north of Cape Hatteras and then south along the coast appear to be essential prerequisites for successful homing to South Atlantic rivers. In contrast, shad returning to North Atlantic rivers during the spring are not obliged to follow a coastal route because offshore temperatures in the Middle Atlantic Bight are well within the shad's range of oceanic occurrence (Figure 9). However, tag returns from adults tagged on spawning runs into North Atlantic rivers indicate that many (most?) adults do enter coastal waters in the lower mid-Atlantic region and migrate north along the coast to reach home rivers as repeat spawners the following spring (Talbot 1954; Leggett 1977). Results of Atlantic coast tagging are consistent with our upper temperature limit (15°C) for shad migration at sea; all prespawning, oceanic migrants enter inshore waters as far south as North Carolina. The significance of the Cape Hatteras region to other aspects of northern versus southern shad biology was discussed by White and Chittenden (1977).

Based on our proposed migratory route, large shad catches in ICNAF Division 6B during the spring would consist of shad entering home rivers and populations moving toward and along the coast. Catches in Chesapeake Bay and the sounds of North Carolina from late November to early December (Hildebrand and Schroeder 1928; Talbot and Sykes 1958; Walburg and Nichols 1967)

[11]Isakov, V. I. 1976. The peculiarities of diurnal vertical migrations of mackerel in the northwestern Atlantic. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. No. 111, Serial No. 3934, 3 p.

[12]Rikhter, V. A. 1976. Proposal on trawling surveys for estimation of pelagic fish stocks in ICNAF Subarea 5 and Statistical Area 6. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1976, Res. Doc. No. 116, Serial No. 3939, 3 p.

[13]Cohen, E. B. 1975. An overview of the plankton communities of the Gulf of Maine. Int. Comm. Northwest Atl. Fish. Annu. Meet. 1975, Res. Doc. No. 106, Serial No. 3599, 16 p.

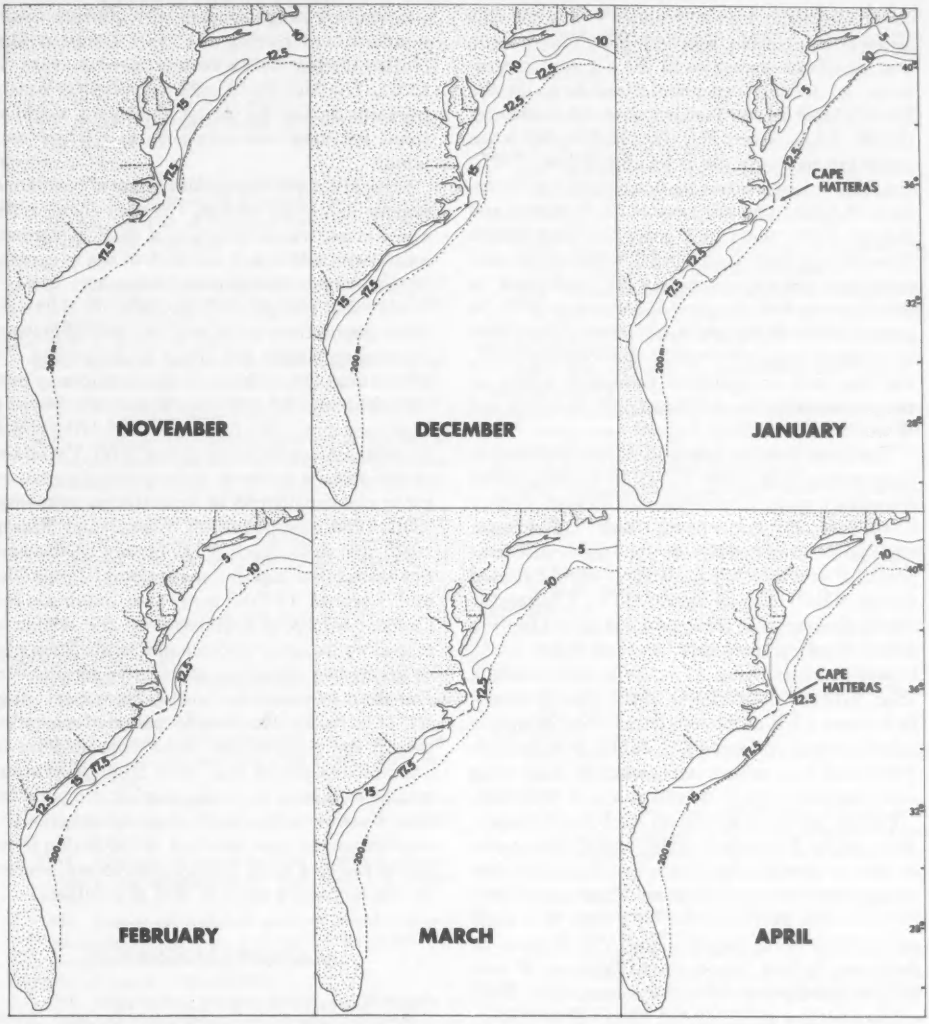

FIGURE 9.—Mean monthly bottom temperatures during winter and spring along the eastern U.S. coast, Cape Cod, Mass., to Florida. (From Walford and Wicklund 1968.)

would be shad returning to natal rivers farther south. Inshore temperatures are unstratified along the Atlantic coast during the winter (Parr 1933). Since freshwater discharge generally occurs along the surface from estuaries, water temperatures would not preclude near-surface movements of shad to detect essential olfactory and rheotaxic cues for successful homing (Dodson and Leggett 1974).

Estuarine temperatures from initial to peak arrival of shad at home rivers along the Atlantic coast are between 3° and 15°C (Talbot 1954; Massmann and Pacheco 1957; Walburg and Nichols 1967; Leggett 1972; Leggett and Whitney

1972; Chittenden 1976; Sholar[14]). Within this temperature regime, southern populations begin reaching home estuaries at the higher temperatures, while northern populations do so at the lower temperatures. Peak numbers of shad enter the St. Johns River, Fla., in mid-January when water temperatures are at an annual low of 15°C; the peak in juvenile emigration occurs simultaneously (Leggett and Whitney 1972; Williams and Bruger 1972). Shad first enter the Connecticut River in late March-early April when water temperatures are approximately 4°C and peak in abundance at 13°C (Leggett and Whitney 1972). In general, most shad populations north of Cape Hatteras begin entering rivers at approximately 4°C, and the peak in upstream migration occurs at temperatures between 10° and 15°C (Leggett and Whitney 1972).

The lower thermal tolerance of juvenile shad in freshwater was near 2.2°C in a short-term laboratory study (Chittenden 1972) and roughly 3°-4°C in small outdoor ponds (Blair[15]). This lower thermal limit agrees closely with the lowest temperature at which subadult shad were collected during NMFS offshore surveys (3°C). Chittenden (1972) also reported that juveniles ceased feeding when water temperatures dropped below 4.4°C. However, we collected 17 juvenile and subadult shad (9-32 cm FL) during a NMFS coastal survey in January 1978, at stations with bottom temperatures between 2.8° and 4.3°C. All but one stomach were filled with mysids and copepods, indicating active feeding at these temperatures in saltwater.

Further evidence to support our bottom temperature regime for predicting the coastal movements of shad is provided by North Carolina's anadromous fishery research program. Their annual surveys on river herring since 1971 show that shad occur off the North Carolina coast from January to April, at bottom temperatures between 6° and 12°C and at depths <26 m (Johnson et al.[16]). Shad catches decline substantially when water temperatures exceed 12°C, coinciding with entry into estuaries or possibly, northward migration. This temperature range concurs with offshore bottom temperatures having the most frequent shad catches during NMFS bottom trawl surveys (7°-13°C). The shallow depths traveled by coastal migrants during the winter and spring would account for their unavailability to offshore sampling.

Critical data on the oceanic phase of most anadromous fishes are lacking (Harden-Jones 1968), and our general description of shad movements must await additional research at sea to corroborate or correct the proposed migratory cycle. It would seem energetically wasteful for North Atlantic populations to follow the same shoreward route as do Middle and South Atlantic shad. The return of all populations to this region may have historical significance, since shad are believed to have been most abundant in the mid-Atlantic portion of their coastal range (Leim 1924). Variations in life history patterns among populations are generally considered to be adaptive responses (Cole 1954; Murphy 1968; Gadgil and Bossert 1970), and differences in life history characteristics among shad populations in rivers (Carscadden and Leggett 1975b) may also exist at sea. Endocrine-induced differences in the timing of migratory behavior and gonadal maturation may be life history strategies of adaptive significance, considering the species' wide geographical range (21° of latitude). The lengthy period of migration toward the mid-Atlantic coast from offshore by prespawning adults may stem from population-specific responses to photoperiod or temperature cues. Further study on the sensory systems and environmental cues involved in migration is required before a more comprehensive explanation for the migratory cycle of shad is available.

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[15]Blair, A. B. 1977. American shad culture and distribution studies at Harrison Lake National Fish Hatchery. Proc. Workshop American Shad, Amherst, Mass., Dec. 1976, 10 p.

[16]Johnson, H. B., B. F. Holland, Jr., and S. G. Keefe. 1977. Anadromous fisheries research program, northern coastal area. Section II. N.C. Proj. AFCS 11-2, 41 p.

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SOURCES AND DISTRIBUTION OF BLUEFISH, *POMATOMUS SALTATRIX*, LARVAE AND JUVENILES OFF THE EAST COAST OF THE UNITED STATES

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ABSTRACT

Larval bluefish are found offshore somewhere between Cape Cod, Mass., and Palm Beach, Fla., during every season of the year. However, there appear to be two main spawning concentrations—one during spring near the western edge of the Gulf Stream in the South Atlantic Bight and the other during summer over the continental shelf of the Middle Atlantic Bight. Larvae complete development near the surface; juveniles are strongly associated with the surface. Juveniles from the spring spawning remain at sea and are carried northward past Cape Hatteras, N.C., above the edge of the continental shelf. As surface shelf water warms, they move shoreward to spend the summer in estuaries of the Middle Atlantic Bight. Bluefish spawned in summer remain at sea as juveniles or enter estuaries briefly in late summer. In fall, as the water cools, the juveniles move southward out of the Middle Atlantic Bight. It is possible that these two spawnings represent different populations. A smaller fall and winter spawning which occurs offshore south of Cape Hatteras may represent a small population resident to the South Atlantic Bight.

Bluefish, *Pomatomus saltatrix* (Linnaeus), occur in most temperate coastal regions of all world oceans (Briggs 1960). Fowler (1944) erroneously reported them from the eastern Pacific where they do not occur. The earliest descriptions of eggs and larvae of bluefish by Agassiz and Whitman (1885) which have been quoted by other authors, e.g., Padoa (1956) and Salekhova (1959), are erroneous. Colton and Honey (1963), Deuel et al. (1966), and Norcross et al. (1974) correctly described them and showed that bluefish spawn pelagic eggs in the open sea and larval development takes place near the surface. Juveniles generally move from the open sea to coastal areas and estuaries. This pattern has been observed off North America, in the Black Sea, and off South Africa (Irvine 1947; Bigelow and Schroeder 1953; Oben 1957; Smith 1961).

Along the Middle Atlantic Bight, i.e., from Cape Cod, Mass., to Cape Hatteras, N.C., bluefish eggs, larvae, and juveniles have been collected during several ichthyoplankton studies (Sette 1943; Lund and Maltezos 1970; Norcross et al. 1974). Although restricted in sampling area or time, these studies have indicated that spawning and larval development take place offshore from Chesapeake Bay to southern New England in late spring and summer. Juveniles occur in estuaries along the middle Atlantic coast in summer (Clark[3]).

The sources of data for this paper are plankton collections taken by personnel of the National Marine Fisheries Service (NMFS), NOAA, Sandy Hook Laboratory, as part of a study to investigate the importance of estuaries as nursery areas of Atlantic coast fishes. The first part of this study consisted of a survey of ichthyoplankton over the continental shelf, an area thought to be the spawning grounds for many species of fishes. From information gained during this study, we hoped to trace the movement of young stages from spawning grounds and thus evaluate the importance of estuaries as nurseries. From the results of this study, several additional short cruises were conducted to study further the distribution of larval and juvenile bluefish in certain offshore areas at specific times of the year.

In this paper, information from these studies and those of previous workers is presented to help elucidate the times and places of bluefish spawn-

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[3]Clark, J. R. 1973. Bluefish. *In* A. L. Pacheco (editor), Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic coast estuaries, p. 250-251. Middle Atl. Coastal Fish. Cent., Tech. Publ. 1.

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ing along the east coast. Evidence to link the offshore occurrences of bluefish larvae to the estuarine occurrences of bluefish juveniles also is presented. This early life history information relates to what is known of the number and relative sizes of populations of bluefish along the east coast.

MATERIALS AND METHODS

(Table 1, Figure 1)

An ichthyoplankton study of Atlantic continental shelf waters by the Sandy Hook Laboratory began in 1965-66 with a survey from Cape Cod to

TABLE 1.—Bluefish collections from RV *Dolphin* ichthyoplankton surveys and supplemental cruises for young bluefish off the east coast of the United States.

Continental shelf area	Dates	Number of stations	Gear[1]	Bluefish		
				Number of collections	Number	Standard lengths (mm)
Cape Cod to Cape Lookout	3-15 Dec. 1965	78	Gulf V			
		35	MWT			
	25 Jan.-9 Feb. 1966	86	Gulf V	1	1	8.7
		0	MWT			
	6-22 Apr. 1966	92	Gulf V			
		3	MWT			
	12-24 May 1966	92	Gulf V	5	25	3.4-9.1
		63	MWT			
	17-29 June 1966	92	Gulf V			
		59	MWT	2	2	33-37
	5-26 Aug. 1966	92	Gulf V	25	1,621	2.4-13.2
		66	MWT	4	8	9-128
	13-18 Sept. 1966	30	Gulf V	2	2	4.0-6.7
		15	MWT			
	28 Sept.-20 Oct. 1966	92	Gulf V	1	2	3.3-4.0
		77	MWT	1	17	26-219
	9 Nov.-4 Dec. 1966	92	Gulf V			
		68	MWT	2	2	49-124
New River, N.C., to Palm Beach, Fla.	15-19 Feb. 1966	26	Gulf V	1	1	8.0
	7-15 May 1967	80	Gulf V	20	563	2.2-11.6
		80	SMN	11	14	18-34
		80	2-m ring			
	22 July-1 Aug. 1967	80	Gulf V			
		80	SMN			
		53	MWT			
	19-26 Oct. 1967	80	Gulf V	5	17	3.9-6.9
		80	SMN			
		77	3-m ring			
	27 Jan.-4 Feb. 1968	80	Gulf V	2	2	5.1-6.0
		80	SMN			
		50	MWT	2	5	63-92
New York Bight	10-16 June 1969	44	SMN			
		46	MWT	1	1	45.1
		15	Nightlight	1	1	45.9
	15-18 June 1970	44	SMN	3	3	20.8-35.0
		44	2-m ring	1	1	31.3
New Jersey to Maryland	14-18 June 1971	32	SMN	5	8	23.8-33.7
		32	Haedrich	5	7	23.6-32.1
		12	MWT	3	3	27.3-35.7
Virginia to North Carolina	27 Apr.-5 May 1971	58	SMN	19	163	12.6-31.4
		60	Haedrich	27	1,464	3.9-33.5
		19	2-m ring	3	10	4.1-11.3
Cape Hatteras, N.C.	weekly, 11 Apr.-31 May 1972	36	Haedrich	21	1,472	3.5-25.4
New Jersey to Virginia	29 Oct.-1 Nov. 1970	35	SMN	3	3	40.0-48.2
		35	Haedrich	3	4	36.4-34.9
		11	2-m ring	1	3	~200
Georgia to Florida	29-31 Jan. 1971	24	SMN			
		24	Haedrich			
		24	MWT			

[1]MWT = midwater trawl; SMN = surface meter net; see text for further details.

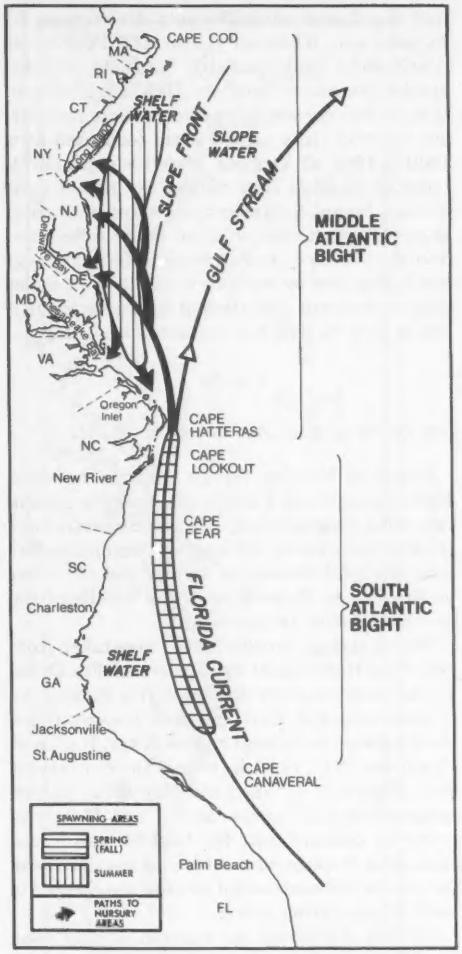


FIGURE 1.—Major features of surface waters and bluefish larval and juvenile distribution off the U.S. east coast.

Cape Lookout, N.C. Over the year, as weather permitted, 92 stations over 14 transects were sampled during 8 cruises. In 1967-68, the study continued, working from Cape Fear, N.C., to Palm Beach, Fla., sampling at 80 stations over 14 transects during each of 4 seasonal cruises. Plankton was sampled with Gulf V samplers (0.52-mm mesh). The 30-min step oblique tows were made at 2.1-2.6 m/s. Two nets were towed simultaneously; one from the surface to 15 m, the other from 18 to 33 m where water depths permitted. Details of gear, procedures, and physical, plankton volume, and juvenile fish data have been published (Clark et al. 1969, 1970).

The same procedures were followed on two additional cruises in 1966. One of these (D-66-2) sampled 26 stations on five transects between Jacksonville, Fla., and Palm Beach in February 1966. The other (D-66-11) sampled 30 stations on the four northernmost transects (Cape Cod to New Jersey) in September 1966.

Collections for pelagic juvenile fishes were made during the cruises in 1965-66 with a scaled-down Cobb midwater trawl (Clark et al. 1969). During the cruises in 1967-68, several nets were towed for juvenile fishes. At each station a surface meter net with 6-mm mesh was towed beside the ship. Subsurface samplers included the scaled-down Cobb trawl, and a 1-m and a 2-m ring net (Clark et al. 1970).

Several offshore cruises from 1969 through 1971 were designed mainly to augment the data on occurrences of bluefish juveniles. A surface meter net and a Haedrich neuston net (Bartlett and Haedrich 1968) were used in paired tows on most of these cruises. Other sampling equipment used at various times included dip nets with nightlights and several types of midwater nets.

In spring 1972, a series of eight weekly cruises near Cape Hatteras aboard a chartered sport fishing boat was conducted working from Oregon Inlet, N.C., out into the Gulf Stream. On each cruise, we made two neuston tows with a Haedrich net near Cape Hatteras. One of these was in the green coastal water, the other in the blue Gulf Stream water, and each tow was within 100 m of the interface between the two water masses. During the return to Oregon Inlet, some 60 km north of Diamond Shoals Light Tower, several additional tows sampled the full range of surface water temperatures occurring in the area. Weather and water temperature data relative to these cruises were gathered from the U.S. Naval Oceanographic Office and the U.S. National Weather Service.

Additional data on bluefish and juveniles and ancillary observations from these collections are available.[4]

[4]Kendall, A. W., Jr., and L. A. Walford. 1978. Data associated with offshore larval and juvenile bluefish collections at Sandy Hook Laboratory 1965-1972. Unpubl. manuscr., 5 p. Report No. SHL 78-9. Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

We will generally refer to bluefish <10 mm standard length (SL) as larvae and those >10 mm SL as juveniles. Bluefish hatch at about 3 mm SL and by 10 mm SL the fin ray development is nearly complete and in living specimens the body is dark blue on the back and silvery on the sides, as in the pelagic juvenile stage of goatfish and mullet (Norcross et al. 1974).

RESULTS

Hydrographic Features of Middle and South Atlantic Bights

Shelf water characterized by salinities of <35‰, is divided into coastal water (<33.6‰) and shelf edge water (33.6-35.0‰) (Wright and Parker 1976). The Gulf Stream, characterized by salinities >36.0‰ and/or temperatures >18°C at 100 m or >15°C at 200 m, flows generally beyond the edge of the continental shelf. The water mass between the shelf water and Gulf Stream, called the slope water, is separated from the shelf water by a strong surface feature, except in midsummer, called the slope front. Surface manifestations such as lines of flotsam, differences in water color, and choppiness of the Gulf Stream are seen on moderately calm days. The shelf water is sluggish and influenced by short-term effects of wind, but generally moves south along the shore. The Gulf Stream moves northward or northeastward at velocities over 100 cm/s (Sverdrup et al. 1942).

Eggs

Bluefish eggs, which share features with pelagic eggs of many other species, were not found in any of our collections. Bluefish eggs have a smooth spherical membrane, a diameter of 0.90-1.20 mm averaging 1.00 mm, a pigmented yolk, a single oil globule about 0.2 mm in diameter, and melanophores in rows on the embryo (Deuel et al. 1966). Even though an egg has all of the above features, it can be identified with certainty as being a bluefish egg only if the oil globule is pigmented and in later development the number of myomeres has become established at 24 to 28.

Two studies have reported occurrences of bluefish eggs along the east coast. Marak and Colton (1961) listed a few of them from late May to early June 1953 in 12.8°C water south of Cape Cod. These data are suspect because: 1) identification was based on inadequate descriptions by Agassiz and Whitman (1885) and Perlmutter (1939); and 2) adult bluefish in spawning condition are not present off southern New England until later in the year when temperatures are considerably warmer. In a second study conducted from 1960 to 1962 off Virginia, Norcross et al. (1974) reported bluefish eggs during the period June through August from near shore to the continental slope. Although none occurred in our collections, from the similarity in distribution of bluefish eggs and larvae seen by Norcross et al. (1974), it seems that an accurate indication of spawning location can be derived from the capture of small larvae.

Larvae

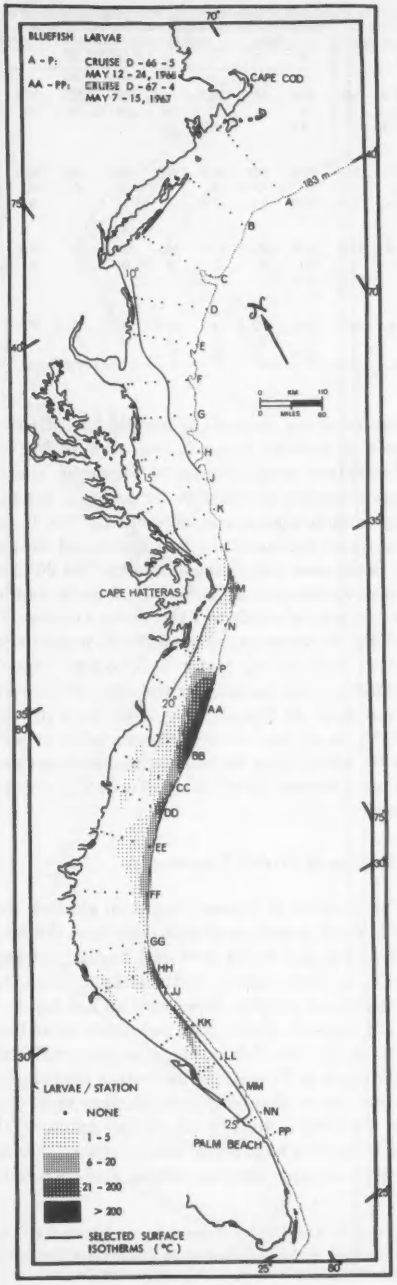
Seasonal-Geographic Distribution

Although bluefish larvae occurred between Massachusetts and Florida during every season, two major geographically distinct concentrations of larvae were found; one south of Chesapeake Bay near the Gulf Stream in spring, and the other north of Cape Hatteras over the middle of the continental shelf in summer.

During spring, bluefish larvae were taken from near Cape Hatteras to Cape Canaveral, Fla. Of the 473 larvae taken at 25 stations during the surveys of May 1966 and 1967, greatest concentrations were between the offings of New River, N.C., and Charleston, S.C., near the edge of the continental shelf (Figure 2). In April and May 1971, we also caught bluefish larvae near Cape Hatteras primarily offshore near the Gulf Stream. From these data, it appeared that bluefish spawned near the edge of the continental shelf in the South Atlantic Bight during spring.

Bluefish dominated the neuston catches near Cape Hatteras during the eight weekly cruises in spring of 1972 (Table 2). They occurred on every cruise and in every water type sampled. The variability in catches between paired tows during this series was too large to permit precise comparison among the dates or sampling areas. However, the largest catches were made in water just shoreward of the Gulf Stream. Most of the specimens taken in or near the Gulf Stream were between 5 and 12 mm SL, whereas the few taken over the shelf ranged from 11 to 21 mm SL.

The numbers of bluefish caught each week gave no indication of relative abundance during spring in this area, partially because weather-influenced



surface temperature patterns affected the catch rate. Large catches just shoreward of the Gulf Stream followed periods of northerly winds which caused a compression of surface isotherms in this area. Following southerly winds the isotherms were spread out and catches were low. It thus appears that the catch rate was related to the width of the band of suitable water, and that in turn was related to wind conditions.

No bluefish larvae were collected in the Middle Atlantic Bight in January, April, May, and June 1966, but they were abundant and widespread in August when their distribution extended from eastern Long Island, N.Y., to Virginia and more or less over the breadth of the continental shelf (Figure 3). They were most abundant off New Jersey and Delaware. Most of these larvae were small (mean, 4.0 mm SL) indicating that spawning had occurred not long before this cruise. The relative number of fish <4 mm SL was greatest at the northern end of the survey area and diminished progressively southward to Delaware Bay (Figure 4). This effect could have resulted from growth of the larvae during our sampling from north to south in this area over a 3-day period. It also might have resulted if bluefish spawning had started in the south and progressed northward. Either or both of these processes may have been involved. There was an 11-day gap in sampling between Delaware Bay (Transect F) and Maryland (Transect G). This might account for our finding so few, but larger larvae south of Delaware Bay.

Bluefish spawning in middle Atlantic waters was almost finished by the end of summer, judging from the paucity of specimens taken during September and October (Figure 5). In September, when we sampled only north of middle New Jersey, we caught two larvae; and in October, when the sampling area extended over the whole Middle Atlantic Bight, we again caught two. We have no information on the southerly extent of bluefish larvae during September, since there was no sampling south of New Jersey then.

Four bluefish larvae were taken during winter cruises, one at each of four stations near the edge of the continental shelf. One was taken off North Carolina (Transect N) and the other three between St. Augustine, Fla., and Palm Beach (Transects Y, KK, and LL).

FIGURE 2.—Distribution of surface temperatures and larval bluefish in May. Transects A-P sampled May 1966; AA-PP sampled May 1967.

TABLE 2.—Bluefish catches in paired neuston nets during eight weekly cruises off Cape Hatteras, N.C., April, May 1972.

Item	11 Apr.		18 Apr.		27 Apr.		4 May		11 May		16 May		23 May		31 May	
	Tow 1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Gulf Stream:																
Surface temperature (°C)	22.0	ND	23.3	ND	22.5	22.4	23.5	ND	24.0	ND	25.1	ND	ND	ND	25.5	ND
Bluefish catch	0	0	7	0	12	218	8	0	4	0	0	0	0	0	0	0
Mean length (mm SL)			10.9		8.9	10.0	11.6		9.8							
200 m shoreward of Gulf Stream:																
Surface temperature (°C)	16.0	ND	19.5	20.6	13.2	22.1	20.0	18.6	20.3	ND	22.6	ND	ND	ND	20.5	19.5
Bluefish catch	4	0	41	14	93	771	3	2	4	0	6	0	0	0	35	217
Mean length (mm SL)	4.8		11.1	10.0	5.5	9.9	12.3	9.1	10.6		12.0				5.9	16.3
Intermediate (shelf) water:																
Surface temperature (°C)	12.5	ND	10.6	11.7	ND	ND	15.4	17.0	18.0	16.1	19.4	ND	15.1	ND	17.3	16.3
Bluefish catch	0	0	0	0	0	0	0	1	17	0	2	0	0	0	0	0
Mean length (mm SL)								21.4	12.9		18.7					
Nearshore:																
Surface temperature (°C)	13.0	ND	10.8	ND	ND	ND	ND	ND	16.0	ND	19.5	20.0	ND	ND	19.0	ND
Bluefish catch	0	0	0	0	0	0	0	0	5	0	2	0	0	0	0	0
Mean length (mm SL)									10.7		18.8					

[1]No data.

Temperature-Salinity Regimes

During the survey, bluefish larvae occurred in two distinct temperature-salinity regimes. One regime was characterized by surface temperatures of 18°-26°C and salinities of 30-32‰ (Figure 6). These conditions prevailed from late spring through the summer above the thermocline in coastal waters of the Middle Atlantic Bight. Bluefish spawning evidently did not begin there until late July or early August, judging from the small number of large larvae taken in August. Thus, spawning of bluefish in the Middle Atlantic Bight seemed to be influenced partly by features of environment other than temperature and salinity.

The other regime was associated with the inner edge of the Gulf Stream and was characterized by surface temperatures of 20°-26°C and salinities of 35-38‰. As mentioned above, few bluefish larvae occurred in this water during the fall and winter, considerable numbers during the spring, and none during the summer.

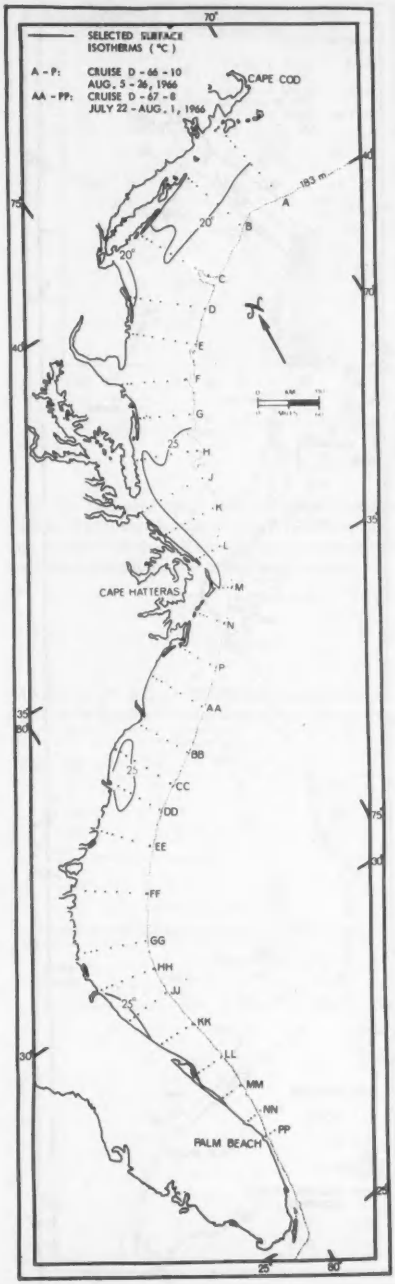
Seasonal Surface Temperature Relations

Regardless of season or area, nearly all larvae were taken in waters between 17° and 26°C. Larvae appeared on the shelf throughout the South Atlantic Bight in spring where the surface water temperatures ranged from 19° to 24.5°C. North of Cape Hatteras where we took no larvae in spring, shelf water was <15°C, but near the edge of the Gulf Stream where we did take larvae, temperatures were >15°C. At the stations where bluefish larvae were taken during August, surface temperatures ranged from 18.8° to 25.7°C. Surface water covering most of the Middle Atlantic Bight south of eastern Long Island was within this temperature range (Figure 3). However, south of Cape Hatteras no bluefish larvae were taken in July when temperatures were mostly >26°C. Surface water temperature had decreased between our September and October cruises. The 20°C surface isotherm was off Long Island in September, but had moved south to Virginia by October. The bluefish larvae were taken in 20.3°C water in September and 16.4°C water in October. The few bluefish larvae taken near the edge of the continental shelf off Florida in October were in water >25°C. In winter, all occurrences were in water >20°C, which was limited to the outer portion of the continental shelf from North Carolina to Florida at that time.

Diel Cycles of Vertical Distribution

The number of larvae caught in shallow tows (0-15 m) when compared with deep tows (18-33 m) during day and night provided limited information about diel cycles of vertical distribution. The catch rate was highly dependent on net depth. At the 46 stations where both nets were towed and either caught bluefish larvae, more occurred in the shallow net at 37 stations indicating that the larvae were more abundant in the shallow layer (sign test, $P<0.001$). Nearly all of the catch of the deeper net may have occurred as it passed through the surface layer during setting and retrieving.

FIGURE 3.—Distribution of surface temperatures (left) and larval bluefish (right) in July-August. Transects A-P sampled August 1966; AA-PP sampled July-August 1967.


SELECTED SURFACE ISOTHERMS (°C)
A - P: CRUISE D - 66 - 10 AUG. 5 - 26, 1966
AA - PP: CRUISE D - 67 - 8 JULY 22 - AUG. 1, 1966
CAPE COD
CAPE HATTERAS
PALM BEACH
183 m
A
B
C
D
E
F
G
H
J
K
L
M
N
P
AA
BB
CC
DD
EE
FF
GG
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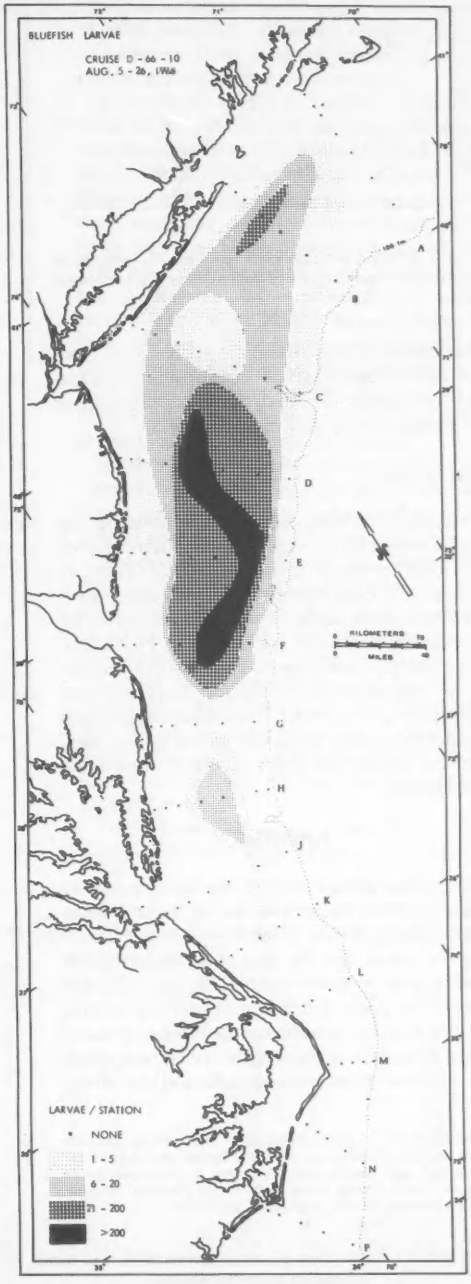
MM
NN
PP
20°
25°


BLUEFISH LARVAE
CRUISE D - 66 - 10
AUG. 5 - 26, 1966
KILOMETERS
MILES
LARVAE / STATION
NONE
1 - 5
6 - 20
21 - 200
>200

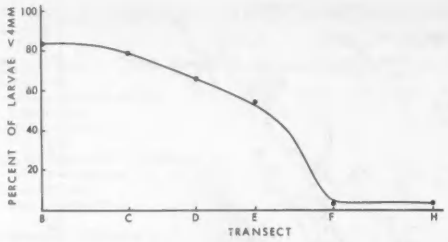


FIGURE 4.—Percent of bluefish larvae <4 mm SL captured on transects B-H (Figure 2) in the Middle Atlantic Bight in August 1966.

Indeed, later studies (Kendall and Naplin[5]) have shown that bluefish larvae occur primarily within 6 m of the surface. The distribution of catches was similar during day and night (Table 3).

Larval Lengths

The length distribution of larvae taken in the shallow tows was not significantly different from that taken in deeper tows (χ^2 $P > 0.05$) (Table 4). This result is to be expected if, as indicated above, the catches in the deeper tows can be accounted for by contamination in the surface layer. Fish taken during the day, however, were generally smaller (2.5-4.5 mm) than those taken at night (5.5 mm and larger) (χ^2 $P < 0.001$). This effect could result from net avoidance by larger larvae during daytime. The cruises were too infrequent to estimate larval growth.

Juveniles

During the survey cruises we tried to collect pelagic juvenile fishes and during later cruises tried to clarify results from the surveys by sampling in areas and during seasons in which juveniles had occurred earlier. We took bluefish juveniles in several kinds of midwater and surface nets. It is difficult to compare the catches of these several nets or the catches made in different years; nevertheless, this limited information about

[5]Kendall, A. W., Jr., and N. A. Naplin. Diel-vertical distribution of bluefish (*Pomatomus saltatrix*) larvae and that of associated fish eggs and larvae. Manuscr. in prep. Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732.

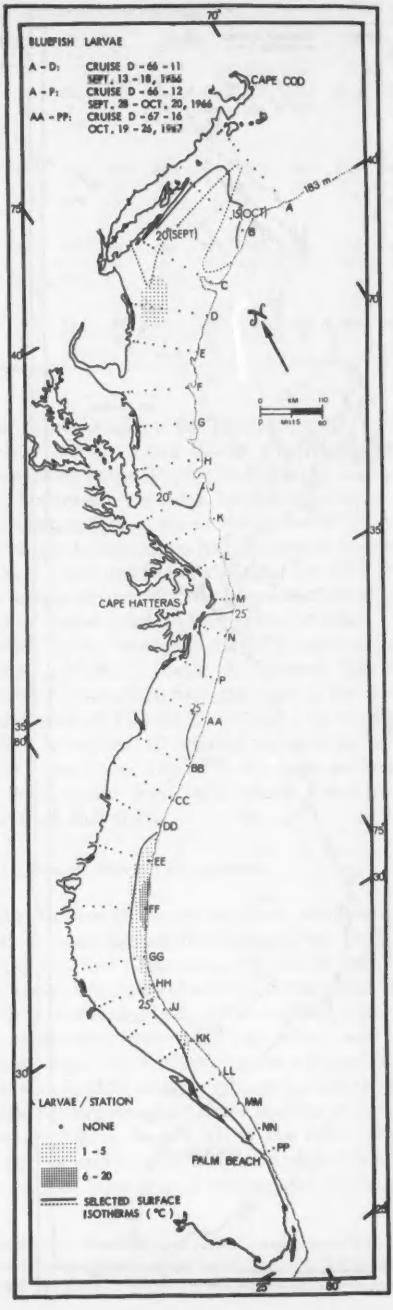

BLUEFISH LARVAE
A - D: CRUISE D - 66 - 11 SEPT. 13 - 18, 1966
A - P: CRUISE D - 66 - 12 SEPT. 28 - OCT. 20, 1966
AA - PP: CRUISE D - 67 - 16 OCT. 19 - 26, 1967
CAPE COD
183 m
20 (OCT.)
20 (SEPT.)
CAPE HATTERAS
PALM BEACH
LARVAE / STATION
NONE
1 - 5
6 - 20
SELECTED SURFACE ISOTHERMS (°C)

FIGURE 5.—Distribution of surface temperatures and larval bluefish in September-October.

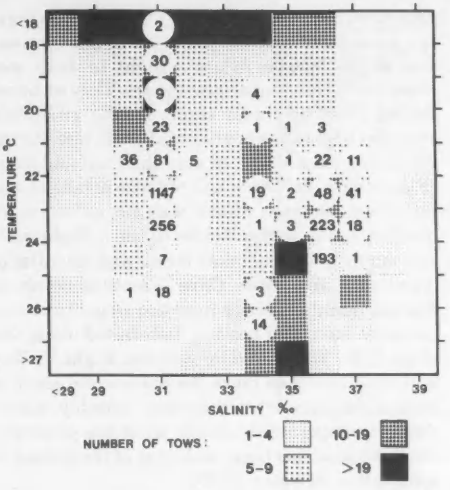


FIGURE 6.—Clustering of catches of larval bluefish by temperature-salinity combination during RV *Dolphin* surveys, 1965-68. Numbers of bluefish larvae superimposed on temperature-salinity combinations where they were caught.

TABLE 3.—RV *Dolphin* 1965-68 ichthyoplankton survey. A comparison of bluefish larval catches during day and night.

Larvae/tow	Number of tows: Day	Night	χ^2	
1	12	8	0.309	
2-10	6	7	0.303	
11-100	7	7	0.080	
>100	3	2	0.078	
Totals	28	24	0.770	(3 df; $P > 0.80$)

offshore seasonal geographic distribution of bluefish juveniles indicates a complex pattern of movements from offshore spawning areas to coastal and estuarine nursery areas.

In summary we found bluefish juveniles, presumably from the spring spawning, at the surface near the slope front from south of Cape Hatteras to off the Middle Atlantic Bight in April to June (Figure 1). We hypothesize that they move northward along the slope front, then cross the shelf, enter estuaries of the Middle Atlantic Bight and after spending the summer in the estuaries, return to the sea and move southward along the coast and out of the Middle Atlantic Bight. Some juveniles from the summer spawning in the Middle Atlantic Bight remain in coastal waters while some enter estuaries briefly. They too leave the Middle Atlantic Bight in early fall. The following is our evidence for these conclusions.

In May 1967, juvenile bluefish were scattered over the continental shelf in the South Atlantic Bight and north to Cape Hatteras (Figure 7). The largest specimens were from stations near shore.

In April and May 1971, we sampled the offshore area intensively around Cape Hatteras to find any trace of young bluefish which could be attributed to larvae and juveniles such as had appeared previously to the south. During this cruise neuston tows took bluefish juveniles near the edge of the continental shelf (100-fm (183-m) isobath) (Figure 8a). All of the specimens taken were in water >15°C, which occurred all across the shelf south of Cape Hatteras, but only near the edge of the shelf north of there.

In the June 1966 survey, when 59 stations were sampled, bluefish appeared at each of two widely

TABLE 4.—RV *Dolphin* ichthyoplankton surveys 1966-68. Length distributions of larval bluefish collected in Gulf V samples.

Interval midpoint (mm SL)	South Atlantic Bight: Winter D-66-1	Winter D-66-2	Winter D-68-1	Spring D-66-5	Spring D-67-4	Fall D-67-16	Middle Atlantic Bight: Summer D-66-10	Summer D-66-11	Summer D-66-12	Shallow tows	Deep tows	Day	Night	All data
2.5					97		231			301	27	266	62	328
3.5				4	205	8	610		2	739	89	689	139	828
4.5					128	6	515	1		602	49	371	280	651
5.5			1	4	15	1	136			145	12	72	85	157
6.5			1	2		2	21	1		22	5	11	16	27
7.5				5			11			14	2	7	9	16
8.5	1	1		8			5			13	2	10	5	15
9.5				2	1		5			7	1	2	6	8
10.5							10			10			10	10
11.5					1		1			2		1	1	2
12.5							1			1			1	1
13.5							1			1			1	1
23.5					1					1			1	1
Total	1	1	2	25	448	17	1,547	2	2	1,858	187	1,429	616	2,045
Mean				6.88	3.63	4.31	4.00			3.98	3.88	3.73	4.51	3.97
Variance				3.55	1.61	0.96	1.31			1.58	1.26	0.84	2.78	1.55

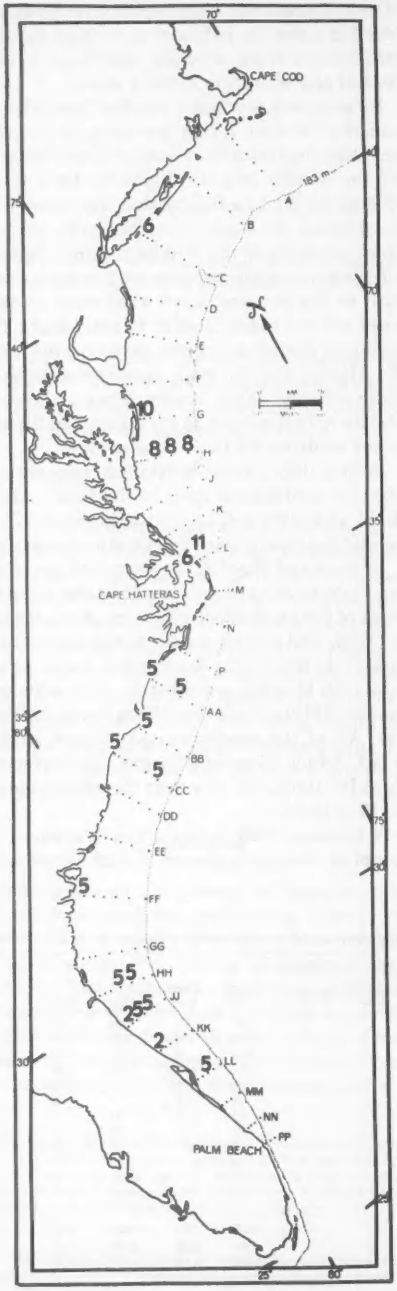


FIGURE 7.—Months of capture (indicated by numerals) of juvenile bluefish at stations sampled by surface meter net and midwater trawl during RV *Dolphin* surveys, 1965-68.

separated nearshore stations (Figure 7). The regular presence of bluefish juveniles in offshore waters of the Middle Atlantic Bight in June was observed in three subsequent years. They occurred during 1969 only near shore; during 1970 only near the edge of the continental shelf; and during 1971 they were scattered over the shelf and slope (Figure 8b, c, d). The origin of these juveniles was puzzling, because there was no evidence of bluefish larvae in the Middle Atlantic Bight until midsummer. We had taken larvae and juveniles in April and May from Cape Hatteras south to Florida mainly offshore near the slope front. Apparently these fish become distributed along the slope front off the Middle Atlantic Bight in May and June and then cross the continental shelf in June as surface waters become suitably warm. Surface temperatures on the shelf are generally 15° to 20°C at this time, and most of the juveniles were taken in water >18°C.

The juveniles we caught in August (Figure 7) were presumably products of recent spawning in nearby waters, for only slightly smaller larvae appeared in the plankton tows in the same area. One specimen 128 mm SL taken just outside Chesapeake Bay had probably been spawned in the spring off the South Atlantic Bight.

We collected a few juveniles of widely differing sizes during two surveys in fall 1966. In a cruise conducted in 1970, we confirmed the regular presence of juvenile bluefish in the Middle Atlantic Bight in fall. We then collected juveniles between Delaware and Chesapeake Bays within 13 km of the shore (Figure 8e); and several specimens about 200 mm SL in the same area. The juveniles from these cruises can be attributed to the summer spawning of bluefish in continental shelf waters of the Middle Atlantic Bight; and the fish about 200 mm SL to the southern spring spawning. The latter fish had presumably spent the summer in middle Atlantic estuaries (Wilk[6]) and had returned to the ocean. A 124-mm SL specimen taken in November may have originated from either spawning.

No bluefish juveniles were taken in fall in the South Atlantic Bight and neither larvae nor

[6]Wilk, S. J. 1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Sandy Hook Lab. Tech. Ser. Rep. 11, 56 p.

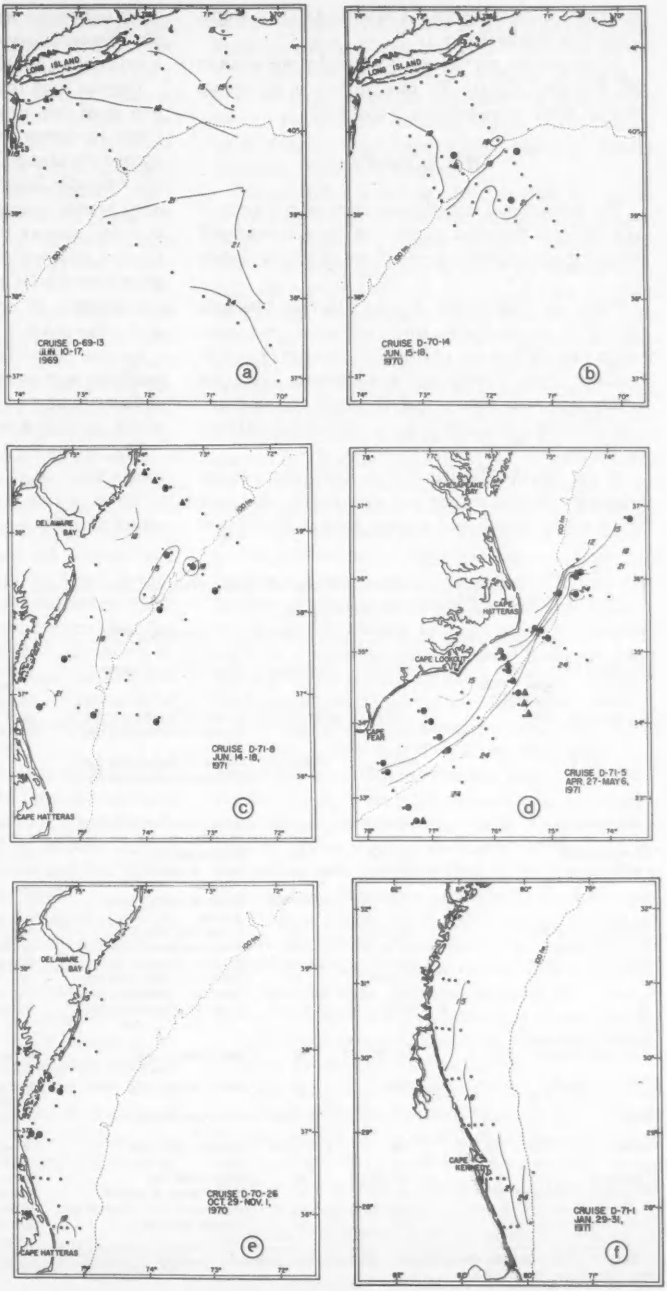


FIGURE 8.—Distribution of juvenile bluefish and surface temperatures during six cruises over portions of the Middle Atlantic Bight. Sampling stations indicated by dots. Presence of juvenile bluefish in surface meter net or Haedrich net indicated by circles, in midwater trawls by triangles, and under nightlight by a star.

juveniles were taken in the Middle Atlantic Bight from late fall to June.

In the winter survey, a few juveniles were taken off Florida (Figure 7), but during a follow-up cruise, none were caught (Figure 8f).

DISCUSSION

The patterns of distribution of young stages of bluefish off the east coast can be summarized based on our collections and those of others (Table 5).

From our collections of small larvae, bluefish appear to spawn in two quite different areas—in water just shoreward of the Gulf Stream (Florida Current) from Florida to Cape Hatteras, i.e., the South Atlantic Bight, and in shelf water from Cape Hatteras to Cape Cod, i.e., the Middle Atlantic Bight.

In the South Atlantic Bight, spawning occurs primarily during spring and apparently also to a lesser extent in fall and winter. Most of the larvae we caught were well offshore just shoreward of the Gulf Stream in water which was 20°-26°C and had a salinity of 35-38‰.

Larvae from the spring spawning in the southern area are evidently carried northward past Cape Hatteras in April and May and become spread out along the continental slope off the Middle Atlantic Bight. As shelf waters become suitably warm, generally in mid-June, the young bluefish appear to cross the shelf and enter estuaries, where they spend the summer. There they grow from 25-50 mm SL to 175-200 mm SL (Wilk see footnote 6) and in early fall migrate south along the coast.

Larvae from the fall and winter spawning in southern waters may find their way inshore south of Cape Hatteras as indicated by a few juveniles which we found in Florida in winter.

The spawning in the Middle Atlantic Bight in continental shelf waters occurs in summer. The water in which larvae were found here was 3°C cooler and 5‰ less saline than that in the south-

TABLE 5.—Collections of bluefish eggs, larvae, and juveniles, east coast of United States.

Reference	Sampling period: Years	Sampling period: Months	Sampling area	Occurrences of bluefish	Numbers	Lengths (mm)
Eggs:						
Marak and Colton (1961); Marak, . . . , Foster (1962); Marak, . . . , Miller (1962)	1951-56	Feb.-June	Ocean off New England	Late May-early June 1953 south of Martha's Vineyard	few	
Norcross et al. (1974)	1959-60	all except Oct.	Ocean off Chesapeake Bay	June, July, August 1960 and 1961		
	1961-62	all	Ocean off Chesapeake Bay	July 1962, nearshore to slope waters	many	
	1962	seasonally	Ocean off Chesapeake Bay			
	1963	July, Aug.	Ocean off Chesapeake Bay			
Larvae:						
Sette (quoted by Perlmutter 1939)	1929	Apr.-July	Ocean from Cape Cod-Chesapeake Bay	40°N-Chesapeake Bay; waters near 21°C; mostly outer half of shelf	many	3-21
Herman (1963)	1957-58	all	Narragansett Bay	July, 20.7°C	1	3
Lund[1]	1965	May, July-Sept.	Ocean off eastern Long Island	July-Sept. (most in Aug.)	73	5-30
	1966	June-Sept.	Ocean off eastern Long Island		981	5-20
de Sylva et al. (1962)	1956-58	all	Indian River Inlet, Del.	Aug.-Sept.	2	4-28
Pearson (1941)	1929-30	all	Lower Chesapeake Bay	24 July, at mouth of bay	4	4-7
Norcross et al. (1974)	1959-60	all except Oct.	Ocean off Chesapeake Bay	May-Aug.	34	3-7
	1961-62	all	Ocean off Chesapeake Bay	July-Sept.	441	3-11
	1962	seasonally	Ocean off Chesapeake Bay	July	34	5-14
	1963	July, Aug.	Ocean off Chesapeake Bay	July-Aug.	93	4-22
Juveniles (<100 mm):						
Pearcy and Richards (1962)	1959-60	all	Mystic River, Conn.	Seined, July-Aug. lower estuary	2	75-94
Perlmutter (1939)	1938	all	Waters around Long Island	Throughout summer—small fish trawl	6	78-96
Lund[1]	1968	July-Sept.	Shinnecock Bay, N.Y.	Throughout summer—seined small (40 mm) fish in July and Aug.	200	40-100
de Sylva et al. (1962)	1958	every other	Delaware River, Del.	Seined, June-Sept. lower estuary	130	30-100
Pacheco and Grant (1965)	1957-58	all	White Creek, Del.	Seined, May-June, Sept.	45	39-104
Richards and Castagna (1970)	1965-66	all	Eastern shore of Virginia	Trawled, at inlets, July, Sept.	5	31-85
Tagatz and Dudley (1961)	1957-60	all	Shoal waters near Beaufort, N.C.	Seined, May-July; Oct.-Nov.	37	40-100
Turner and Johnson (1973)	1970	all	Newport River, N.C.	Surface, trawled, upper river May, July, Oct.	few	45-72

[1]Lund, W. A., Jr. Early life history of the bluefish, *Pomatomus saltatrix* (Linnaeus), off the coast of New York and southern New England. Contrib. 64 Mar. Res. Lab., Noank, Conn., 23 p.

ern area (18°-26°C and 30-32‰). Bluefish larvae have been reported by other authors in this area from May through September, but mostly in July and August (Table 5). Larvae have also been reported in the more saline areas of several estuaries of the Middle Atlantic Bight (Table 5). Although some juveniles from the Middle Atlantic Bight spawning inhabit estuaries in late summer, more seem to remain along the shore. Nevertheless, all appear to move southward and out of the bight in midfall. Their distribution in late fall and winter is still unknown.

From the scarcity of juveniles (i.e., fish 50-150 mm SL) in our samples at sea, and the abundance of these fish in estuarine collections, it appears that bluefish depend chiefly on estuaries for habitat during this stage. Their dependence is determined by the time and place of their spawning. Those from the spring spawning spend most of their first summer in estuaries, while those from the summer spawning spend at most about a month there. Both changes in temperature and seasonal photoperiod influenced the activity and distribution of adult bluefish at least under laboratory conditions (Olla and Studholme 1971, 1972). Thermal edges may act as barriers affecting the distribution of juvenile bluefish, as shown in recent laboratory work (Olla[7]). These factors, and possibly others, probably trigger movements of juveniles from the open ocean to estuaries and back to the open ocean.

In order to assess the relative proportions of the two major spawning areas to the total recruitment of bluefish on the Atlantic coast in any given year, it would be necessary to sample repeatedly during the spring south of Cape Hatteras and during the summer in the Middle Atlantic Bight.

Our present limited understanding of early life history contributes to several other facets of bluefish biology. Population differences of bluefish on the U.S. Atlantic coast have been studied using meristic characters (Lund 1961), migratory patterns, morphometrics, and scale morphology (Wilk see footnote 6). All of these studies indicate that more than one population exists. Scale studies defined two groups of bluefish by the size of fish when the first annual ring forms in May. One group, which reaches about 260 mm by the end of its first winter, evidently represents fish spawned in spring south of Cape Hatteras. The other group, which reaches only about 120 mm by the end of its first winter, represents fish spawned in the summer in the Middle Atlantic Bight. Body proportions of these two groups of fishes are statistically different (Wilk see footnote 6).

Precise information on adult bluefish migration is not available, but general patterns are known (Wilk see footnote 6). Some mature bluefish spawn near the inner edge of the Gulf Stream as they migrate northward from their wintering grounds off Florida. To a lesser extent some bluefish also spawn in the same area in fall and winter, presumably on their return migration. Adult bluefish migrate to coastal waters off the Middle Atlantic Bight in spring and feed there until they migrate south coincident with fall cooling. During their stay in the Middle Atlantic Bight, bluefish spawn on the shelf, and to some extent in mouths of the larger estuaries (Norcross et al. 1974). Although spawning can take place as soon as the adults arrive in the area in May, most seems to occur in July and August, while some continues into September. From the apparent annual variations in timing and amount of this spawning, it is dependent on a combination of several features of the environment including temperature, salinity, photoperiod, and food for the adults.

If each mature fish spawns in both areas and in all seasons, this would indicate that there is a single stock of bluefish on the east coast of the United States. If each fish spawns in only one area, separate populations must exist. Our early life history information is consistent with other information that indicates that there are separate populations. Southern and northern spawnings take place under quite different hydrographic conditions and in quite different current regimens to assist the young fish in movements to nursery grounds. In time these conditions could allow genetically distinct populations to become established. Tagging and fecundity studies would show to what extent this has happened.

Since year-class strength of fishes is determined mainly during their young stages, it is important to understand the factors influencing survival of these stages. In bluefish, the eggs and larvae occur at the surface of the ocean and the juveniles occur in estuaries, areas affected by annual variations in weather-related phenomena and, to an increasing extent, affected by man's activities. It is thus important to monitor these influences and

[7]B. L. Olla, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. August 1978.

develop models to relate them to year-class strength of the various spawnings of bluefish.

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CONTRIBUTION OF 1960-63 BROOD HATCHERY-REARED SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, TO THE COLUMBIA RIVER COMMERCIAL FISHERY

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ABSTRACT

A 4-yr marking program was conducted at Leavenworth National Fish Hatchery, Leavenworth, Wash., to determine the contribution of hatchery sockeye salmon, *Oncorhynchus nerka*, to the Columbia River commercial fisheries and the economic feasibility of hatchery rearing of sockeye salmon. The study involved 1960 through 1963 brood-year fish. During the 4-yr period, 1961-64, a total of 11.5 million fish were released, of which 3.4 million were marked by the removal of the adipose fin and part of one of the maxillary bones—the right maxillary for 1960 and 1962 broods and the left maxillary for 1961 and 1963 broods. Trapping at the lake outlet in the spring for the first 2 yr indicated that less than 50% of the stocked fingerlings migrated. In 1964-67, recovery of marks from the commercial fishery on the Columbia below and the Indian fishery above Bonneville Dam showed that an average of 13.6% of the sockeye salmon catch was composed of fish raised at Leavenworth Hatchery. Adjusting for effects of marking, this represents an average fishery value per brood of $4,274.75. The average potential benefit/cost ratio for the 4 yr of the program was 0.04 to 1. Because preliminary data indicated such a low benefit/cost ratio, sockeye salmon rearing at Leavenworth was radically decreased in 1966 and terminated in 1969.

In the 1930's Grand Coulee Dam was constructed on the upper Columbia River, thus barring anadromous fish runs from 1,835 km of spawning and rearing area. The extreme height of the dam (106 m) precluded building passage facilities for both upstream and downstream migrants. To preserve the runs formerly utilizing the upper basin, a relocation of runs of affected species became necessary.

Basic data on existing fish populations were obtained from 1933 through the time of dam completion in 1941 (Fish and Hanavan 1948). The only relocation areas suitable for spawning and rearing were Columbia River tributaries below Grand Coulee Dam and above Rock Island Dam. The area was less than one-half the extent of that formerly available and on streams which, because of industrial diversion, were for the most part inaccessible to migrating fish. Because of general depletion of all the upriver salmonid runs, correction of fish passage problems was already underway in many areas. With the impetus of the relocation program, further rehabilitation was accomplished.

The sockeye salmon, *Oncorhynchus nerka*, was seriously affected by the habitat changes as its development required a lake-stream environment which has been almost completely eliminated. Annual commercial catches of Columbia River sockeye salmon ranged from ½ to 2 million kg prior to 1900 (Gangmark and Fulton 1952). From then through the early 1920's annual catches varied from about ¼ million to over 1 million kg. Following one more good year in 1926, the ½ million kg figure was never again reached (Figure 1).

Estimates of escapement beyond the fishery were not possible until enumeration of migrating adults began in 1933 at Rock Island Dam, 755 km above the mouth of the Columbia River. An average of about 19,000 adults was counted annually until 1941, when only 949 adults passed upstream. The low escapement was caused by a large commercial catch, low flows, and retention of water behind Grand Coulee Dam (Fish and Hanavan 1948).

The relocation of runs began in 1939 for sockeye salmon as well as chinook salmon, *O. tshawytscha*; coho salmon, *O. kisutch*; and steelhead trout, *Salmo gairdneri*. Adult sockeye salmon were trapped at Rock Island Dam and were transported by tank trucks to the Wenatchee and Okanogan

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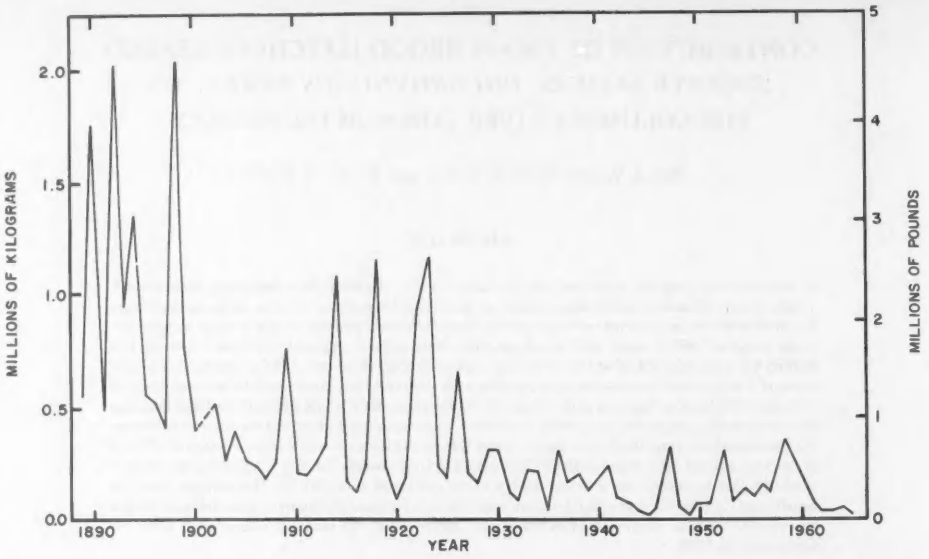

FIGURE 1.—Commercial catch of sockeye salmon in the Columbia River, 1889-1967. [Data for 1889-1936 from Craig and Hacker (1940), for 1937 from Ward et al. (1963) and for 1938-67 from Fish Commission of Oregon and Washington Department of Fisheries (1968).]

Lakes where they were allowed to spawn naturally (Figure 2).

Supplementary to adult relocation, an artificial propagation program was planned. A hatchery was constructed on Icicle Creek, a tributary of the Wenatchee River near Leavenworth, Wash. (Figure 3). Smaller substations were built on the Entiat and Methow Rivers. The sockeye salmon production program was to be concentrated at Leavenworth National Fish Hatchery.

Fish produced at Leavenworth were stocked into Wenatchee and Osoyoos Lakes. Success of the sockeye salmon relocation program was indicated in 1947 when the largest run recorded since 1926 appeared. This raised the question of whether the remaining available spawning habitat was overpopulated, prompting annual inventories that continued for many years (Gangmark and Fulton 1952).

How much of the apparent improvement in sockeye salmon runs was attributable to hatchery production was unknown. Importance of the Wenatchee system for total sockeye salmon production was obvious. Data indicated that an average of 33% of upper Columbia River sockeye salmon homed to the Wenatchee River in the 7 yr just prior to this study (French and Wahle 1965).

Wenatchee System Sockeye Salmon Stock

For over 25 yr Leavenworth Hatchery produced sockeye salmon which were stocked and reared in Wenatchee River tributaries. During this time, five major dams were built on the main Columbia River downstream. These structures, combined with growth and expansion in population and industry, added greatly to existing problems which confronted both downstream migrants and returning adults.

The Wenatchee River system was historically an excellent salmon producing system. It was comparable, for sockeye salmon production, to the Arrow Lakes, Yakima Basin, and Okanogan Lake areas, formerly the primary producers of this species in the basin (Figure 2). In the early 1900's the runs in the Wenatchee became severely depleted because of construction of impassable mill and power dams and unscreened irrigation projects. These conditions prevailed until the early 1930's, at which time about 85% of the Columbia

FIGURE 2.—Portion of Columbia River Basin showing areas of past and present importance to sockeye salmon as described in text.

River run was being produced in the Arrow Lakes area (Fulton 1970).

The Grand Coulee Fish-Maintenance Project (Fish and Hanavan 1948) began in 1933. Under this project, obstructions were removed, dams were provided with passage facilities, and irrigation diversions were screened. These measures were necessary to establish suitable habitat for the relocated runs in tributaries between Grand Coulee and Rock Island Dams.

To reintroduce sockeye salmon to the spawning areas above Lake Wenatchee and provide eggs for

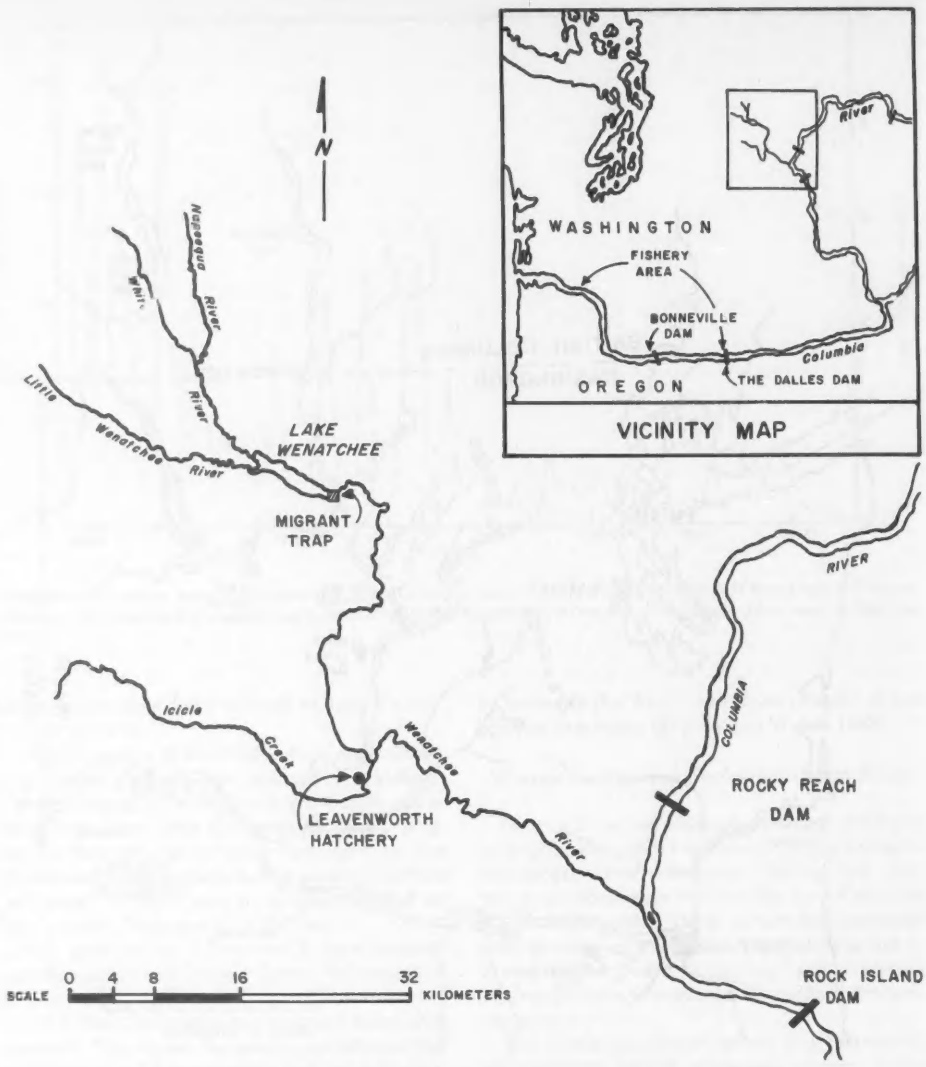

FIGURE 3.—The Wenatchee River system and location of Leavenworth National Fish Hatchery.

Leavenworth Hatchery, adult fish were trapped from 1939 through 1943 at Rock Island Dam on the main Columbia. Because the proposed hatcheries would not be available to handle fish until 1940, adults of all displaced species were released for natural spawning in predetermined locations. Separate areas were selected for each species to prevent overcrowding and mixing. Most of the sockeye salmon transplanted undoubtedly originated in the Arrow Lakes, but fish from the Okanogan and Wenatchee systems were certainly included (Fulton 1970).

Under the Grand Coulee Fish-Maintenance Project, sockeye salmon adults were trapped in July and August and hauled by tank truck to Lake Wenatchee, 113 km above Rock Island Dam, where a barrier was installed at the outlet. When spawning time approached, the fish ascended the White and Little Wenatchee Rivers where they spawned. When eggs were later needed for hatchery use, weirs were installed and adults trapped to supply the required ova. Surplus adults were allowed to pass upstream and spawn naturally. The offspring of these natural spawners homed back to the system to establish the new Wenatchee stock.

Spawning occurred in September and October. The fry emerged from the gravel in spring and drifted back down to the lake to rear until the following year. Outmigration occurred in April and May, with a peak reached in early May prior to the heavy spring run-off period (French and Wahle 1959). Following 2, or occasionally 1 or 3, yr at sea, the adults entered the Columbia River in late spring. The run passed Bonneville Dam in late June and early July, and several weeks later ascended the Wenatchee River to renew the cycle.

The Hatchery

Leavenworth National Fish Hatchery was completed in 1940 as the primary station to provide hatchery-reared fish to supplement the newly established natural runs. Sockeye salmon were to be produced there and adults of other species were spawned to obtain stock to supply the satellite stations on the Entiat and Methow Rivers (Figure 2). The hatchery capacity was approximately 3.5 million eggs and 2.4 million fingerlings (Fish and Hanavan 1948).

The source of eggs for the first 5 yr of operation was fish that had been hauled to Lake Wenatchee from Rock Island Dam as part of the relocation project. After this period the adult transportation was terminated and spawning operations continued using fish returning to the lake naturally.

After the eggs were taken and fertilized, usually in September, they were transferred to the hatchery for incubation. Hatching began in January and the fry began to feed about 6 wk later. Initial rearing took place inside the hatchery, and when water temperatures became suitable, they were placed in outside rearing ponds. In September or October, upon reaching an average weight of 9 to 10 g, the fingerlings were trucked to the lake. Survival from egg to stage at release ranged from 62 to 96%. After wintering over until the following April or May, the smolts migrated out of the lake.

From general observations, it appeared that the hatchery operation was a success: proper rearing techniques were followed, hatchery migrants were observed leaving the lake, adults returned to the area in adequate numbers, and fish were available for commercial harvest. Data obtained through spawning surveys and downstream migrant counts at the dams indicated that the sockeye salmon population was being satisfactorily maintained. However, it was not possible to determine whether the wild stock or the hatchery fish contributed most to the runs. Downstream migrant studies by Anas and Gauley (1956) pointed out the impossibility of identifying the separate stocks.

There were indications that the costs of conducting a sockeye salmon hatchery program were significantly higher than the values contributed to the fishery. Despite complexities of measurement of runs, some means of assessment seemed necessary. Thus, a study was designed to evaluate the economic feasibility of continuing artificial propagation of sockeye salmon at the hatchery.

The study involved the marking of a proportion of the hatchery sockeye salmon production for a period of 4 yr, observations on the rearing and migration of the fingerlings, and estimation of the contribution of returning adults to the commercial fishery. An analysis of production costs and the monetary benefits to the fishermen was included.

FIELD OPERATIONS

Estimating Procedures

The procedures used in making estimates of numbers of fish are similar to those described in reports by Worlund et al. (1969) and Wahle et al. (1974). Estimates of the potential contributions and value of hatchery sockeye salmon required four steps: 1) estimation of marked and unmarked hatchery releases, 2) estimation of catch of marked adults, 3) estimation of total contribution of hatchery fish to the catch, and 4) application of dollar values to the estimate of contribution.

Marking and Release Procedure

The study began in July 1961, using 1960-brood fingerling sockeye salmon. Each year, approxi-

mately one-third of the total Leavenworth Hatchery stock was marked. In each year except the first, a circular net pocket with a metal sleeve and a tub sampler were used to obtain a sample of fish for marking. Two types were employed: a 3-pocket sampler which gave an approximate 33.3% sample for marking, and a 10-pocket sampler (Worlund et al. 1969; Wahle et al. 1974) which provided a 10% sample for population estimate. In 1961, the one-third sample was obtained by marking every third pond, and in the other 3 yr the fish to be marked were selected as described above.

In 1961, hatchery personnel marked 1,008,310 1960-brood sockeye by removing the adipose fin (Ad) and part of the right maxillary bone (RM). In 1962, the 1961-brood fish (600,036) were marked by removal of the adipose fin and part of the left maxillary bone (LM). The 1962-brood fish (1,146,485) were marked the same as the 1960-brood, and the 1963-brood (606,578) repeated the 1961-brood mark.

In 1961 the marked and unmarked fish were kept in separate ponds and mortality records kept for each group. The number of unmarked fish for release was estimated by using the number of eggs and the percentage of hatch, and subtracting the number marked plus pond mortality. As the fish were stocked, in order to avoid bias, the marked and unmarked fish were mixed in each truck load.

In the three following years, by knowing the actual number of fish marked for each brood year, and the postmarking mortality, the total population at release time was estimated. Using the 10-pocket sampler on a random group of fish from a pond, a 10% sample was obtained. Repeating this procedure on the 10% sample provided a 1% sample, and a Peterson index of sample size was calculated (Table 1). The fingerlings were transported by tank truck and released into Lake Wenatchee each fall.

TABLE 1.—Numbers of sockeye released into Lake Wenatchee, Wash., during marking program.

Brood	Mark[1]	No. marked	No. unmarked	% marked	Total released
1960	Ad-RM	1,000,725	1,760,319	36.24	2,761,044
1961	Ad-LM	571,726	1,327,878	30.10	1,899,604
1962	Ad-RM	1,247,755	2,554,809	32.81	3,802,564
1963	Ad-LM	570,735	2,504,344	18.56	3,075,079
Total		3,390,941	8,147,350	29.39	11,538,291

[1]Ad = adipose fin; RM = right maxillary bone; LM = left maxillary bone.

In the spring of 1962 and 1963, a trap was operated at the lake outlet to monitor the outmigration. Data obtained at the trap indicated that <50% of the marked fish migrated downstream. This amounted to 38.4% of the marked fish of the 1960-brood and 47.9% of the 1961-brood.

Marked Fish Recovery

Sampling for returning marked adults began in 1964 and continued through 1968. Earlier returns were not expected because prior studies at Lake Wenatchee indicated that few, if any, adults would return in their third year (Major and Craddock 1962). The search for marks was confined to the two commercial fishing areas in the lower Columbia River: zones 1-5, the gill net fishery below Bonneville Dam, and zone 6, the Indian set net and dip net fishery above the dam (Figure 3). Other fisheries were not sampled as Columbia River sockeye salmon rarely occur in the ocean commercial catch and are seldom taken by sport anglers (Koski 1964).

We looked for marked fish during the commercial seasons. The zone 6 catch was monitored at Washington and Oregon Indian fishery buying stations. Commercial canneries in the lower river were sampled for the zones 1-5 gill net catch. Unfortunately for the study, the commercial gill net season in zones 1-5 was closed in 1965 and 1966, and opened only for 5 days in 1964 (Fish Commission of Oregon and Washington Department of Fisheries 1968). The zone 6 catch was also limited by this restriction, severely reducing the total catch (see Table 4). The catch in the 7 yr previous to the study averaged 90,900 fish. During the study period the average was only 22,500 ranging from 4,361 to 56,200 (Figure 4).

Sampling Results

Nearly one-half of the Columbia River commercial sockeye salmon catch was inspected for marks each year, except in 1966 when only a 4.2% sample was obtained because of the erratic nature of landings. The extremely small sample undoubtedly biased the estimation of catch for the brood years involved. For most brood years, the majority of fish were caught in their fourth year (Table 2). For all broods except the 1962 group an average of 94% was caught at age 4_2 (4 - total age, 2 - seaward migration age). This age-group represented only 4% of the total 1962-brood fish caught in 1966, evidence that the age 4_2 fish were almost entirely missed by the fishery, although undoubtedly available.

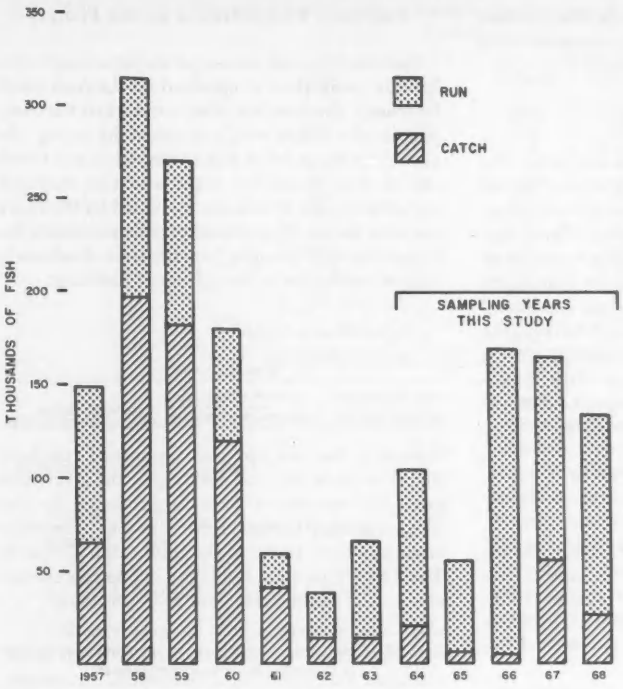

FIGURE 4.—Columbia River sockeye salmon commercial catch in thousands, as part of the total run, 1957-68. [Data from Fish Commission of Oregon and Washington Department of Fisheries (1968).]

TABLE 2.—Sampling rate and marks observed in Columbia River commercial fishery for sockeye 1960-63 broods.

Catch year	Fishery zone[1]	Total catch	Number sampled	Percent sampled	No. of marks observed by brood year			
					1960	1961	1962	1963
1964	1-5	4,950	3,307					
	6	15,820	7,195					
	Total	20,770	10,502	50.6	265	1		
1965	1-5	70	24					
	6	5,773	3,024					
	Total	5,843	3,048	52.2	22	43		
1966	1-5	157	27					
	6	4,204	158					
	Total	4,361	185	4.2		1	8	
1967	1-5	21,218	7,993					
	6	35,002	13,885					
	Total	56,220	21,878	38.9			191	294
1968	1-5	20,300	9,689					
	6	5,000	2,632					
	Total	25,300	12,321	48.7				16
				Total	287	45	199	310

[1]Zone 1-5 (below Bonneville Dam); Zone 6 (above Bonneville Dam).

The number of fish in the catch, the number sampled and the number of marks recovered from zones 1-5 and zone 6, were combined.

CALCULATIONS

Because the marks used to distinguish the groups of hatchery fish have a negative effect on survival, two different steps were employed to calculate the hatchery fish contribution. The determination of the level of contribution required an estimation of the number of hatchery fish in the catch for each year sampled. This was calculated from the estimated number of marked fish plus the estimated number of hatchery unmarked after a correction for differential mark mortality. Potential catch is that which would be expected if marking did not cause postrelease mortalities.

Differential Mark Mortality (Survival Factor)

We suspected that there would be adverse effects on the survival of the fish because of the excised fin and maxillary bone. Foerster (1968) reported that marked sockeye salmon at Cultus Lake had an estimated return of only 38% of the unmarked return.

To obtain a mark survival factor, a modification was made to the procedure for marking the 1961-brood fish. In addition to the group that received an Ad-LM, a second group received only a chemical (tetracycline) mark, while a third had both marks. In sampling returning adults, a comparison of the three groups showed that only 40% of Ad-LM fish expected, returned (Weber and Wahle 1969). Because we believe that tetracycline had no effect on survival, we considered that the difference between returns was caused by mortality due to marking by excision.

Marks in Catch

To calculate the number of marks in the catch for a certain year, the number of n marks in the sample was divided by the sampling ratio:

$$n \text{ marks (catch)} = \frac{n \text{ marks (sample)}}{n \text{ fish (sample)}/n \text{ fish (catch)}}.$$

This assumed a random sample of the catch. The mark survival factor was not considered in this equation.

Hatchery Contribution to the Fishery

To determine the percent of sockeye caught in a specific year that originated at Leavenworth Hatchery, the number of (n) unmarked hatchery fish in the catch was estimated by using the number of (n) marked fish in the catch and dividing by the sampling ratio and the marked/unmarked ratio at release, corrected by the mark survival factor. The correction was necessary because this ratio changes from the time of release to time of catch due to the effects of marking:

$$n \text{ unmarked hatchery catch} = \frac{n \text{ marks (catch)}}{\frac{n \text{ fish (sample)}}{n \text{ fish (catch)}} \times \frac{n \text{ marked release}}{n \text{ unmarked release}} \times \text{survival factor}}.$$

Summing the marked and unmarked hatchery fish for a catch year and dividing by the total catch gave the estimated percent produced by the Leavenworth Hatchery. For 1964-67, contributions averaged 13.6% of the total catch (Table 3). The 21.6% figure for 1966 may not be representative as the sample size that year was small.

TABLE 3.—Estimated numbers and percent of hatchery sockeye in Columbia River commercial catch.

Catch year	Brood year	Hatchery fish				Total catch all fish
		Marked	Unmarked	Total	%	
1964	1960	517	1,504	2,021		
	1961	2	8	10		
Total		519	1,512	2,031	9.8	20,770
1965	1960	42	123	165		
	1961	82	316	398		
Total		124	439	563	9.6	5,843
1966	1961	24	90	114		
	1962	189	638	827		
Total		213	728	941	21.6	4,361
1967	1962	500	1,692	2,192		
	1963	751	5,443	6,194		
Total		1,251	7,135	8,386	14.9	56,220
1968	1963	31	226	257	(1)	25,300

[1]Not applicable as no 1964 brood hatchery fish were marked.

Potential Hatchery Catch

A potential hatchery catch figure is a theoretical number that represents what could have been caught in a given fishery assuming the same effort and no marking program and was required to calculate benefit/cost ratios. It allows for the large number of fish failing to survive because of the mark. Potential hatchery catch (Table 4) was calculated by dividing the number of marks in the catch by the mark survival factor and adding the

TABLE 4.—Potential number and weight of hatchery sockeye by brood year and catch year.

Brood year	Catch year	No. with marks in sample	Hatchery fish in catch		
			Estimated no.	Potential no.	Potential wt[1] (kg)
1960	1964	255	2,021	2,359	4,122
	1965	22	165	192	342
Total		287	2,186	2,551	4,464
1961	1964	1	10	11	16
	1965	43	398	451	802
	1966	1	114	130	234
Total		45	522	592	1,052
1962	1966	8	827	950	1,706
	1967	191	2,192	2,518	4,085
Total		199	3,019	3,468	5,791
1963	1967	294	6,194	6,684	10,733
	1968	16	257	277	479
Total		310	6,451	6,961	11,212
Grand total		841	12,178	13,572	22,519

[1]The average weight of commercially caught sockeye ranged from 1.5 to 1.8 kg during the study.

number of unmarked hatchery fish in the catch:

$$\text{potential hatchery (catch)} = \frac{n \text{ marks (catch)}}{\text{survival factor}} + \text{unmarked hatchery (catch)}.$$

ECONOMIC EVALUATION

A primary purpose of this study was to determine the economic feasibility of rearing sockeye salmon at Leavenworth National Fish Hatchery. An oft-employed measure of financial worth of a program is the benefit/cost ratio which compares the dollar value (benefit) of the fish returned to the amount spent (cost) in their production. Normally a favorable ratio should exceed 1:1.

Cost Accounting

Production costs for each brood of sockeye salmon in this study were derived in the same manner as in Wahle et al. (1974) and consisted of two categories, amortized construction costs or capital costs and operational costs.

The "annual imputed capital charge" was computed by amortizing the capital expenditures at the hatchery into 30 equal annual payments using an interest rate of 3.5%. This rate was the average 3- to 5-yr government bond interest rate weighted by the total annual capital outlay at Columbia River Program Development hatcheries from 1949 to 1970. As the hatchery reared other species in addition to the study fish, the capital charge was apportioned by applying a percentage based on the ratio of manpower time charged specifically to sockeye salmon care.

Operation and maintenance costs were divided into fish food and drugs, and other operational costs. Fish food and treatment costs were apportioned according to the pounds of study fish produced as a percentage of the total production. Other operational costs including labor, personal services, travel, equipment, supplies, and administration were apportioned, as with capital, according to the percentage of time allotted to the care of each brood.

Benefits

In other economic studies involving Columbia River salmonids (Worlund et al. 1969; Wahle et al. 1974) benefits included the accrued values from exvessel prices received by commercial fishermen engaged in the variety of catch methods, i.e., offshore troll, purse seine, gill net, set net, etc. In addition, benefits were calculated for sport-caught fish and for sale of adult carcasses to processors. Our study included only the benefits to commercial fishermen on the Columbia River in the gill net (zones 1-5), and tribal dip net (zone 6) fisheries. Sport catch values were not considered as there are virtually no sockeye salmon caught by anglers in the river.

The simple exvessel price paid to fishermen is a reasonable estimate of benefits as explained by Richards,[2] although some inadequacies exist in more intensive and complicated fisheries. For the minor fishery involved in this study, this method

[2]Richards, J. A. 1969. An economic evaluation of Columbia River anadromous fish programs. U.S. Dep. Int., Fish Wildl. Serv., Bur. Commer. Fish., Working Pap. 17, 274 p.

of valuation seemed satisfactory. The commercial price paid to fishermen during the sampling years ranged from $0.68 to $0.82/kg depending on the area of catch. The benefit/cost ratio averaged 0.039:1, or approximately 4 cents returned for each dollar spent (Table 5).

TABLE 5.—Benefit-cost ratios for Leavenworth sockeye 1960-63 broods.

Brood year	Total catch (kg)	Hatchery fish in catch		Production cost ($)	Potential benefit-cost ratio
		Potential wt (kg)	Potential value ($)		
1960	41,327	4,464	3,062	114,123	0.027:1
1961	49,160	1,052	858	86,823	.010:1
1962	97,228	5,791	4,456	124,321	.036:1
1963	75,579	11,212	8,723	113,541	.077:1
Total	263,294	22,519	17,099	438,808	.039:1

DISCUSSION

As our results clearly show, hatchery fish did not appear significantly in the commercial catch, averaging only 13.5% of the total harvest. Considering that the hatchery fish may have utilized almost one-half of the natural rearing space available, we expected their contribution would be greater. We also expected a larger proportion of hatchery fish in the returning adult run based on the ratio of hatchery to wild smolts emigrating from Lake Wenatchee. In a concurrent study, Craddock[3] determined that hatchery fish made up 53% and 72% of the 1962 and 1963 total outmigration, respectively.

From the economic viewpoint we feel that the study produced an accurate assessment of the benefits provided to the commercial fishermen by the addition of hatchery fish to their catch. We are confident that the method of determining the production costs of the hatchery sockeye salmon provided a valid estimate for that portion of the benefit/cost ratio.

Benefits as a measure of value in this study applied specifically to those received by the commercial fishery. Not considered were intangible benefits derived from the preservation, maintenance, and enhancement of the Columbia River sockeye salmon. The return of adults to the system for a hatchery egg source is another value. Another unmeasured benefit was the contribution to the Indian subsistence and ceremonial fisheries. In short, the total benefits from the Leavenworth Hatchery sockeye salmon program were obviously greater than the value derived within the specific confines of the study.

From the catch results it is apparent that the study period was one of an abnormally low harvest. The river below Bonneville Dam was closed completely for two of the catch seasons and only 5 days fishing allowed in another, with almost all of the small catch taken in the Indian fishery. As the benefits were based on the number of fish provided the commercial fishery, and the zones 1-5 fishermen were almost completely denied the opportunity to harvest these fish, then little in the way of value could be expected under these conditions. It should be noted that the regulatory measures were in effect specifically for the protection of low runs of summer chinook salmon and summer steelhead trout which can be netted at the same time in the area.

Another indication of the unusually low harvest of sockeye salmon during the study period is noted in catch/escapement ratios (C/E), which in the 5 yr preceding the study were 1/1 - 2.6/1. During the study the ratio did not exceed 0.5/1 and ranged downward to 0.02/1 (Fish Commission of Oregon and Washington Department of Fisheries 1968).

In addition to the low rate of return associated with adult harvest, we suspected that poor survival of the released fish through various stages was a primary cause of low adult returns. Problems confronting the young sockeye salmon are discussed below.

We could not assess any effect on the released fingerlings caused by rearing practices at Leavenworth Hatchery, as there was no comparable rearing of sockeye salmon elsewhere. We assumed that the produced fish were of good quality, as the rearing techniques, disease control, and nutrition in effect at the hatchery were essentially the same at other Columbia River salmon hatcheries raising other species.

A possible hatchery-related effect on the quality of the stocked fish may have been undetected disease. As reported by Guenther et al. (1959), a filterable virus disease transmitted by feeding of sockeye salmon carcasses at Leavenworth Hatchery caused extreme mortalities prior to 1954 when the practice was discontinued. Losses from undetected diseases could have had significant effect on survival following release of the fingerlings. Although kidney disease was not detected at the hatchery, prior to release, the senior author observed it in fish held in saltwater during the mark

[3]D. R. Craddock, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Mukilteo, WA 98272, pers. Commun. April 1964.

retention phase of the project. Cumulative long-term effects on outmigrants may have been substantial. Other viral diseases, about which little was known at the time, may have been present.

Lake Existence

A high rate of mortality occurred in Lake Wenatchee during the period of lake rearing, and this was probably spread over the period from stocking until outmigration. Losses similar to the 62 and 51%, found where outmigrants were enumerated, undoubtedly occurred in the 2 yr in which outmigrants were not counted. Foerster (1968) reported that the average smolt migration from British Columbia and Alaska lakes where only fry were stocked was 44% and the survival to return ranged from 11 to 84%. The hatchery rearing at Leavenworth seemed an economic waste, as equal outmigration rates may have been obtained using fry plants.

There is an extensive sport fishery in Lake Wenatchee on Dolly Varden, *Salvelinus malma*, and kokanee, a nonmigrant strain of sockeye salmon. We monitored this fishery in order to determine the effect on released study fish.

Incidental to the trout catch, a fairly large number of sublegal (<6-in) hatchery salmon were taken. This was determined by the presence of marked fish in a sample of sublegal fish in the angler catch. The hatchery fish were caught during the early spring of their second year just prior to their outmigration. Most sublegals were released by the anglers, but mortality undoubtedly resulted from hooking and handling. Additionally, some of the marked sockeye salmon remained in the lake without migrating and were observed throughout the season in the creel checks of legal-sized trout. The percentage becoming resident was unknown, but in 1964 represented 1.4% of the calculated total kokanee sport catch of 17,523 fish.

Sockeye salmon becoming resident in the lake and entering the sport fishery, based on 1964 data, accounted for <1% of the stocked fish. The mortality of sublegal fingerlings from angling was assumed to be small because of their rare occurrence in the sport catch. Health records of the hatchery fish did not indicate any expected loss from disease or parasites. Undoubtedly, the large loss of fingerlings was due to predation by larger fish and possibly starvation.

The heaviest loss of fingerlings in the lake was certainly caused by predation. Although precautions were taken during release, when fish were barged to avoid shoreline concentrations. Thompson and Tufts (1967) reported heavy predation both during and following release periods. Dolly Varden and northern squawfish, *Ptychocheilus oregonensis*, were sampled by gill net and trolling gear. During the weeks of release, the number of captured fish containing sockeye salmon ranged from 58 to 100%. Gangmark and Fulton (1952) during experiments in 1949-51 reported heavy predation by the same species. Our own observations of angler-caught fish from March through July 1962 showed an average of over one sockeye salmon per stomach. No estimate of the total predation loss was possible as the total number of predators was not known.

From our observations and those reported by Allen and Meekin (1973) the zooplankton production in the lake peaked in August and September each year. The hatchery fish, stocked in October, were faced with a declining food supply. Growth apparently stopped during the winter. Fingerlings of the 1961-brood averaged 97 mm FL when stocked in October whereas in the following spring, migrants trapped at the outlet, had a size range of 87-98 mm FL (Weber and Wahle 1969). Low food productivity of the lake, coupled with competition from natural resident fish for food, undoubtedly affected the fitness of the migrant sockeye salmon and possibly caused subsequent losses from stress on the seaward journey.

It is highly improbable that any hatchery production program utilizing an additional rearing period in Lake Wenatchee could succeed. However, even if no loss had occurred during lake residence, thus doubling the number of hatchery outmigrants, no more than a twofold increase in adults could be expected. Even with such an improvement, still more than 10 times that number of adults would be required for a favorable benefit/cost ratio.

Downstream Migrant Problems

With a large portion of the production sacrificed in the lake, the remaining smolts were still faced with great problems. Until recently, little was known of the causes and extent of downstream losses of sockeye salmon, although much information has been obtained for chinook salmon and steelhead trout smolts. Anas and Gauley (1956) studied the seaward migration of sockeye salmon smolts and their data suggested a wide range in

travel time and in size and age of migrants. No estimates of mortality of any given group of sockeye salmon could be made from their data or from other studies conducted at the various dam projects. However, we have assumed that extremely large losses occur in each annual outmigration of sockeye salmon, comparable to those documented for chinook salmon and steelhead trout.

Losses can occur in but a short distance during the seaward journey. Ellis and Noble (1960) reported losses of fall chinook salmon of 12.2 to 29.7% in the Klickitat River in a distance of only 64 km. The Wenatchee stock sockeye salmon smolts had to navigate 844 km in their seaward migration and were subjected to injuries and possible death at each of seven dams, plus the myriad effects of altered flows and water quality.

Major direct causes of mortality in juvenile migrants are gas bubble disease, a result of high dissolved nitrogen concentrations which occur throughout the river and death or injury by passing through turbines (Ebel et al. 1973). At high flows with excessive spill the fingerlings are subjected to the nitrogen problem, while the turbine caused losses are most severe at low flows. Chaney and Perry (1976) reported that the juvenile losses averaged 15 to 20% at each mainstem dam from combined causes. At low flows, cumulative fish losses just from turbine mortality at a series of seven dams may exceed 90%.

Additional mortality can be expected from several other causes. The delay of stream flow in the impoundments has reduced migration rates of juveniles by one-third according to Raymond (1969). The fish are then subject to increased predation, possible loss of marine adaptability, and may become residual in the reservoir. Undoubtedly but a small part of the outmigrants ever reach the sea in some years.

Adult Problems

We surmise that the sockeye salmon suffer losses comparable to the other species in the ocean, but there is no appreciable fishery harvest. The few tagging returns that have been reported for Columbia sockeye salmon (Margolis et al. 1966) indicate a more southerly distribution than for Canadian or Washington sockeye salmon, and there is no inshore marine fishery to intercept the adults.

The relatively few remaining adult sockeye salmon, after surviving the perils of sea life, still must face serious obstacles on the spawning migration. Aside from the commercial harvest, a substantial mortality occurs which cannot be measured precisely. In early reports of upriver fish passage, Schoning (1948) pointed out that annually an average of 36% of the Bonneville Dam count could not be located after subtracting the known harvest. "Fall-back" contributes to the loss and obscures the actual number passing the dam. Later accounts corroborate these losses (Chaney and Perry 1976). Bonneville Dam mortalities would reduce the number of fish available for harvest only in the zone 6 portion of the fishery.

SUMMARY

1. The Columbia River system produced large runs of sockeye salmon prior to 1900, providing an annual commercial harvest reaching 2 million kg.

2. Deterioration of spawning areas and blockage of tributaries caused a severe decline in the sockeye salmon population early in this century.

3. Construction of Grand Coulee Dam in 1941 blocked the sockeye salmon from 1,835 km of spawning and rearing areas, virtually eliminating all natural production.

4. Compensatory measures intended to replace the lost production included relocation of the sockeye salmon runs to suitable areas below Grand Coulee Dam and construction of hatcheries for additional production.

5. Leavenworth National Fish Hatchery on the Wenatchee River was activated in 1940 as the primary fish production station and an annual stocking program of sockeye salmon fingerlings was started.

6. For over 20 yr Leavenworth Hatchery reared sockeye salmon, releasing the fingerlings into the Wenatchee system augmenting the natural production.

7. No assessment had been made of the actual contribution of hatchery fish to the commercial fishery, thus the subject study was initiated using the 1960-63 broods of sockeye salmon.

8. During the initial 4 yr of the study, a total of 11,538,291 fish were released, of which 3,390,941 were marked by removal of the adipose fin and a part of the maxillary bone.

9. The stock used was adult sockeye trapped in tributaries of Lake Wenatchee. Fingerlings were reared at the hatchery until fall, then released into Lake Wenatchee.

10. Surviving smolts migrated out of the lake in the spring. Outmigrant trapping in the first 2 yr

revealed that <50% of the stocked fish migrated downstream.

11. From 1964 through 1968, sampling for marked adults was conducted in the two Columbia River fisheries: the gill net area below Bonneville Dam (zones 1-5), and the Indian set net and dip net fishery above the dam (zone 6). An average of 43.5% of the commercial catch was examined for marks.

12. The commercial harvest was atypical during the study because of regulation restrictions. The average annual harvest for the period was only 22,500 fish compared with average landings of 90,900 for the prior 7 yr. The C/E ratio did not exceed 0.5/1.

13. Almost all hatchery fish in the catch were in their fourth year of life. The average weight of fish in the catch ranged from 1.5 to 1.8 kg.

14. A mark mortality correction factor was included in calculations of hatchery fish in the catch as it was shown that the marked fish survival was only 60.52% of the unmarked fish.

15. During the study, hatchery fish composed an average of 13.6% of the total commercial catch.

16. The exvessel price to fishermen, used to determine benefits in this study, ranged from $0.68 to $0.82/kg.

17. Production costs were determined by a previously developed method utilizing both capital and operational charges.

18. The benefit cost ratio for the study broods was 0.039:1 or about 4 cents returned for each dollar spent.

19. Factors contributing to poor survival of juvenile fish were: high mortality from predation and angling during lake rearing, probable disease and nutritional problems, losses during migration from turbine injury and gas bubble disease, and delay in reservoirs.

20. Reasons for the low return of adults to the fishery include: unknown ocean mortality, losses incurred while ascending Bonneville Dam, and the erratic opportunity of harvest because of season restrictions.

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RELATIVE ABUNDANCE, BEHAVIOR, AND FOOD HABITS OF THE AMERICAN SAND LANCE, *AMMODYTES AMERICANUS*, FROM THE GULF OF MAINE

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ABSTRACT

Meristic characteristics of sand lance taken from Stellwagen Bank indicated the species to be the American sand lance, *Ammodytes americanus*. Bottom trawl data, ichthyoplankton surveys, and diver and submersible observations demonstrated a significant increase in relative abundance of sand lance since about 1975 on Stellwagen Bank; this trend was typical of the Northwest Atlantic from Cape Hatteras, N.C., to the Gulf of Maine. School shapes were constant in appearance, vertically compressed, tightly compacted, and bluntly linear from a dorsal and ventral view. School strengths varied from about 100 to tens of thousands of individuals with the nearest-neighbor distance ranging from ¼ to 1½ body lengths. The swimming motion is sinusoidal in form and eellike in appearance. Swimming speeds varied from 15 to over 120 cm/s. Copepods were the most important food source, constituting 41% of the total weight of food consumed; sand lance feed in school formation between midwater and the surface. Sand lance bury themselves totally or partially in clean sandy substrates when not schooling.

In the Northwest Atlantic, sand lance range from Cape Hatteras, N.C., to Hudson Bay. They occur over sand and fine gravel bottoms and play an important role as a trophic link between zooplankton and commercially important fish such as Atlantic cod, haddock, silver hake, and yellowtail flounder (Scott 1968, 1973; Bowman and Langton 1978). Several species of sportfish (e.g., striped bass and bluefish) also utilize the sand lance as a food source (Bigelow and Schroeder 1953).

Studies of the eggs, larvae, and postlarvae of the American sand lance, *Ammodytes americanus*, have been reported by Covill (1959), Richards (1959, 1965, 1976), Norcross et al. (1961), Williams et al. (1964), and Richards and Kendall (1973). Investigations on the adult sand lance include taxonomic studies by Backus (1957), Richards et al. (1963), Leim and Scott (1966), Reay (1970), Winters (1970), Scott (1972), and Pellegrini[2] and studies on mortality and growth by Graham (1956) and Pellegrini (see footnote 2). Despite these investigations, little is known about the relative abundance, biology, behavior, and food habits of the adult American sand lance.

For the last 10 yr, information has been collected on sand lance during fishery cruises and undersea research programs conducted by the Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, Mass. The purpose of this paper is to describe some aspects of the abundance, behavior, and food habits of the American sand lance based on bottom trawl (groundfish) survey data, observations by scuba divers and from research submersibles with photographic records, and a food-habit study.

MATERIALS AND METHODS

Study Area

The majority of the observations on sand lance were made on Stellwagen Bank, a submarine ridge that rises to within 18 m of the ocean surface on the eastern boundary of Massachusetts Bay (Figure 1). The length of the bank is 39 km (north-south axis) and its greatest width is 13 km (at the southern end). Depths range from 18 to 77 m. Substrate characteristics by depth interval recorded during submersible operations are: 18-43 m—sandy; 43-55 m—sandy bottom with crushed shells; 55-77 m—gravel, rocky with boulders; and below 77 m—mud/silt. Approximately 95% of the bank has a sandy bottom.

Additional observations on sand lance were

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Pellegrini, R. 1976. Aspects of the biology of the American sand lance, *Ammodytes americanus*, from the lower Merrimack River estuary, Massachusetts. Master's problem, Univ. Massachusetts, Amherst, 44 p.

Manuscript accepted September 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

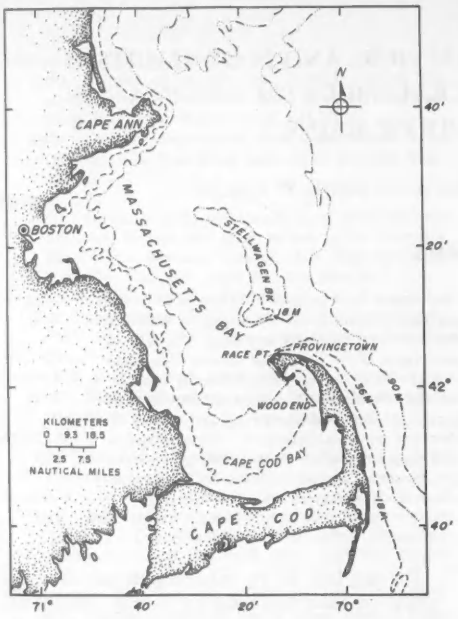

FIGURE 1.—Study area of sand lance observations, Gulf of Maine.

made on the Provincetown slope from Race Point to Wood End (Figure 1). Depths over the Provincetown slope range from 0 to 46 m, with a medium-coarse sandy substrate throughout the range. Slope gradients by depth interval are: 0-9 m—5°-15°; 9-46 m—30°-45°. The relatively steep slope begins between 90 and 250 m offshore.

Relative Abundance

Divers using scuba, or observers in submersibles,[3] made in situ observations during various manned undersea research projects from 1968 through 1977 (Table 1, Figure 2). Camera systems aboard the submersible were: 1) a 35-mm Nikon[4] camera using a 55-mm micro lens and an externally mounted MK 150 Subsea stroboscopic light, and 2) a Sony AD 3400 Monochrome video camera and recorder.

[3]Research submersibles were chartered by NOAA's Manned Undersea Science and Technology Program, Rockville, Md.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Dive locations on Stellwagen Bank and Cape Cod (Provincetown, Mass.) with observations[1] on presence (+) or absence (0) of American sand lance. Observations were made using scuba and submersible (sub).

Dates of observations	Dive sites: Provincetown Scuba	Provincetown Sub	Stellwagen Bank Scuba	Stellwagen Bank Sub
1968	1 - 0			
12-16 July - scuba	2 - 0			
1969	1 - 0			
21-25 July - scuba	2 - 0			
	3 - 0			
1970	1 - 0		5 - 0	
06-09 July - scuba	2 - 0		6 - 0	
	3 - 0			
1971	1 - 0	8 - 0	4 - 0	1 - 0
23-25 June - scuba	2 - 0	9 - 0		2 - 0
22 Sept. - sub	3 - 0	10 - 0		3 - 0
				4 - 0
				5 - 0
				6 - 0
				7 - 0
1972	1 - 0		4 - 0	
18-21 July - scuba	2 - 0		5 - 0	
24-31 Oct. - scuba	3 - 0		6 - 0	
1973	1 - 0		7 - 0	1 - 0
05-10 Oct. - scuba	2 - 0		8 - 0	2 - 0
05-09 Oct. - sub	3 - 0		9 - 0	3 - 0
			10 - 0	4 - 0
			11 - 0	5 - 0
			12 - 0	6 - 0
				7 - 0
				8 - 0
				9 - 0
				10 - 0
1974	1 - 0			
06-11 July - scuba	2 - 0			
	3 - 0			
1976	1 - ++	1 - ++		3 - +
16-18 June - scuba	2 - ++	2 - +		
15-18 June - sub	3 - ++			
1977	1 - +++		4 - ++	
08-11 Aug. - scuba	2 - +++		5 - ++	
	3 - +++			

[1]Estimates of relative abundance are noted as 0 for no sightings, + for a few sand lance observed, ++ for small schools (several hundred individuals per school) with infrequent sightings, and +++ for large schools (thousands per school) and schools observed almost continuously.

Stellwagen Bank is included in one of the sampling strata covered by the spring and fall bottom trawl surveys since 1963 (Grosslein 1969). This stratum encompasses the Massachusetts Bay area, extending from Provincetown to Cape Ann and ranges in depth up to 110 m (Figure 1). Stations were selected randomly within the stratum for each survey and the number of stations actually occupied on Stellwagen Bank on each survey ranged from 0 to 6. Trawl survey results are presented only for 1967-77, the period during which diver and submersible observations were made.

Behavior

Photographic and video records of sand lance behavior were made by scuba divers during a hydroacoustic experiment from RV *Albatross IV*,

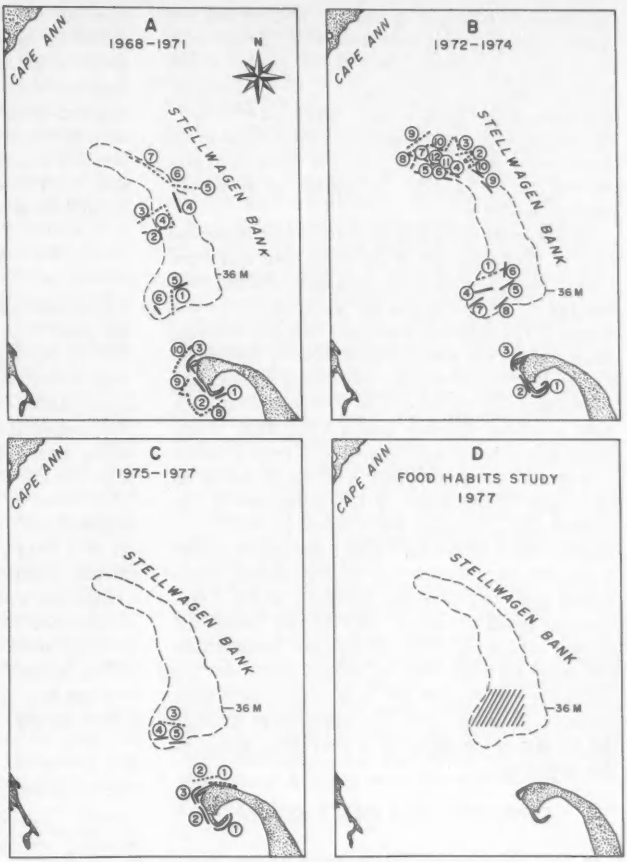

FIGURE 2.—Dive sites and location of 1977 food habits study on Stellwagen Bank and Cape Cod (Provincetown) from 1968 to 1977. Scuba (lines), submersible (dotted lines), 1977 bottom trawl (hatching) sampling areas. See Table 1 for key.

8-11 August 1977, on Stellwagen Bank (scuba dive locations 4, 5) and along the Provincetown slope (scuba dive locations 1-3) (Figure 2C).

Divers, using a Hydro-Products Model 125 television system with a 250-W thallium-iodide light source, filmed sand lance behavior on and near the bottom. The angles and speed at which sand lance entered the bottom substrate and exited from it were estimated from slow-motion video playback.

Schooling behavior was observed and photographed using a Nikonos II underwater camera with a 28- or 35-mm lens and a Subsea MK 150 or 225 electronic strobe. School strength, shape, nearest-neighbor distance, and individual fish size were estimated using in situ observations, photographs, or bottom trawl data. School swimming speeds were estimated at approximately 1 kn by divers swimming parallel to several schools for short distances. A speed of 1 kn is the approximate short-term sustained swimming speed of a diver. All in situ observations by diver scientists were made in daylight between 0900 and 1600 h.

Food Habits

A series of nine tows were conducted from *Albatross IV* on the southwestern edge of Stellwagen Bank over one 24-h period beginning at 1800 h on 9 August 1977 (Figure 2D). The tows were of 5-15 min duration at 3-h intervals and were made with

a Yankee #36 trawl (Grosslein[5]). The cod end and upper belly of the net were lined with 13-mm mesh netting, knot to knot. Only three species of fish were caught in any quantity: spiny dogfish, *Squalus acanthias*; silver hake, *Merluccius bilinearis*; and American sand lance. Sand lance were taken at random from the catch and preserved whole in 10% Formalin for stomach-content analysis.

In the laboratory, the stomachs were dissected out for stomach-content analysis. Ten fish from each of the nine tows were randomly selected from the preserved specimens for analysis. After the stomach was removed from each fish, the contents were examined and washed onto a fine-mesh screen. If the stomach appeared empty or had trace amounts (<1.0 mg) of food in it, it was rinsed out with seawater directly into a Petri dish. When there was a weighable quantity of prey present, the excess water was drawn off by pressing an absorbent tissue paper to the underside of the screen; the contents were weighed and then washed into a Petri dish. Using a dissecting microscope, the prey of each fish were identified to the lowest possible taxonomic grouping, and the percentage composition of each of the identified groups estimated. The percentage composition and total stomach-content weight were used to calculate the percentage weight for each prey category. The data were also expressed in terms of the percentage occurrence of each prey group in the stomachs.

RESULTS AND DISCUSSION

In the taxonomic studies listed above, morphometric and meristic characteristics were used to distinguish between "inshore sand lance" (*Ammodytes americanus* - *Ammodytes hexapterus*) and "offshore sand lance" (*Ammodytes dubius*), although Bigelow and Schroeder (1953) questioned whether such a distinction could be made.

Because of the question regarding the taxonomic status of *A. americanus* and *A. dubius*, several meristic characteristics were evaluated on sand lance caught on Stellwagen Bank (Figure 2D). Dorsal and anal fin ray counts were made directly on 10 randomly chosen fish ranging from 17.9 to 22.2 cm fork length (FL) and averaging 20.0 cm, SD = 1.24. The anal fin ray count ranged from 30 to 31 with a mean of 30.7, SD = 0.48. The dorsal fin ray count ranged from 60 to 63 with a mean of 61.1, SD = 0.99. The vertebral count, based on radiographs of 20 fish and excluding the hypural complex, ranged from 67 to 72 and averaged 69.25, SD = 1.21. The mean values reported here fell into the *A. americanus* category given by Reay (1970). For the purpose of this paper, the classification of Reay (1970) is accepted.

Relative Abundance

Examination of spring and fall survey data for the past 10 yr, excluding 1967, 1969, 1971, and 1973 for spring and 1971 and 1977 for fall (Stellwagen Bank stations were not sampled), indicates a substantial increase in sand lance abundance on Stellwagen Bank (Figure 3). The relative abundance increased during spring cruises from virtually 0 for the 1967-75 period to 50/tow in 1976 and 10,729/tow in 1977, while increasing during fall cruises from 0 for the 1967-74 period to 4,238/tow in 1975 with a decrease to 5/tow in 1976. Spring cruises (March-May) may give a better indication of sand lance abundance since fall cruises are conducted from October to December, a period of lesser sand lance activity before spawning (Winslade 1974). In the Gulf of Maine, all bottom trawl survey catches <75 sand lance/tow occurred on or along the edge of Stellwagen Bank. The catch rate

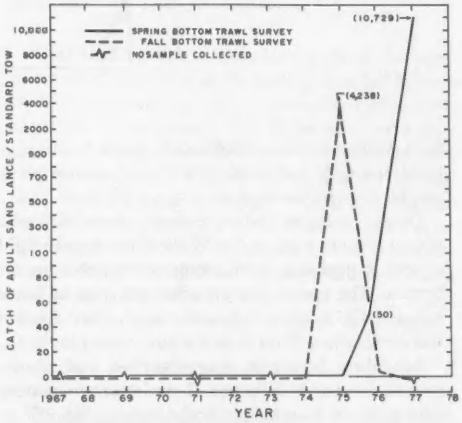

FIGURE 3.—Catch of adult sand lance per standard tow on Stellwagen Bank during the NMFS spring and fall bottom trawl stratified sampling surveys for 1967-77.

[5]Grosslein, M. D. 1969. Groundfish survey methods, NMFS, Woods Hole, Massachusetts. Lab. Ref. No. 69-02, 34 p.

declined drastically, to <1 sand lance/tow, when not fishing on the bank. In the southwest North Sea, fishermen have also noticed that better catches occur along the edges of larger banks and on the tops of smaller ones (Popp Madsen 1963).

In the last 10 yr, sand lance have shown evidence of a population increase along the Atlantic coast from Cape Hatteras, N.C., to and including the Gulf of Maine. Northeast Fisheries Center spring and fall bottom trawl survey results from 1968 to 1977 show large annual fluctuations in sand lance abundance since 1968 with a definite upward trend beginning in 1975 (Figure 4). The magnitude of this increase is considerably less than that recorded on Stellwagen Bank for the same period, but the yearly trends are similar.

One area of concern in attempting quantitative sampling is net avoidance. Livingstone (1962) documented on film that adult sand lance were able to escape in <2.5 s from the cod end of a Yankee Modified #41 trawl net with a cod end mesh of 114 mm, knot to knot, and a 38-mm cotton webbing covering. These films also showed the ease with which individuals and small schools were able to avoid the trawl net. In areas where abundance is high, the ability to avoid trawl nets may be less effective. Scott (1973) found it unusual to catch adult sand lance in nets except in areas where they were very abundant.

Relative abundance of sand lance on Stellwagen Bank and Provincetown slope, based on diver and submersible observations, has increased significantly since 1976 (Table 1). Although numerous diving programs have been carried out over the study area since 1968, it was not until the spring of 1976 that schools of sand lance were first observed. However, it is very likely that relatively small numbers of sand lance were present in the study area prior to 1976 but not noticed by the divers. This increase in sightings coincides with an increase in number of sand lance caught per tow during the bottom trawl survey cruises.

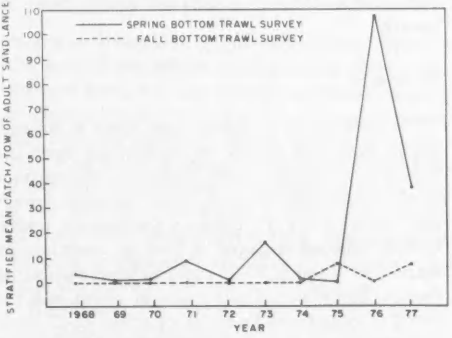

FIGURE 4.—Changes in the relative abundance of adult *Ammodytes* spp. in the Northeast Fisheries Center spring and fall bottom trawl surveys from 1968 to 1977 in the area extending from Cape Hatteras northward. (Data from Grosslein et al. in press, table 3.2.)

Sand lance larvae studies, conducted by the Boston Edison Company[6] showed sand lance larvae were among the most abundant fish larvae occurring in ichthyoplankton sampling surveys conducted in Cape Cod Bay, Mass., during 1974-77. They were more abundant in the eastern portion of the bay and were considerably more abundant in 1976 than in the previous 2 yr. This increase in sand lance larvae was also observed during the Northeast Fisheries Center spring ichthyoplankton surveys conducted in the area from Cape Hatteras to the Gulf of Maine for the past 4 yr (Figure 5). For example, the mean sand lance catch/10 m^2 area in spring 1977 was 9 times greater than in spring 1974.

Bottom trawl survey results, diver and submersible observations, and ichthyoplankton survey results all indicate that there is a relatively large concentration of sand lance inhabiting a small section of the Gulf of Maine, i.e., Stellwagen Bank and outer Cape Cod (Provincetown slope), and that this population has increased considerably since 1975; this increase in population is typical of the Northwest Atlantic from Cape Hatteras to the Gulf of Maine.

Behavior

School Structure

Schools of sand lance observed on the Provincetown slope were relatively small in numbers of fish, ranging from about 100 to several thousand individuals and were usually found in depths ranging from 6 to 20 m. From photographs it was calculated that individual fish on Provincetown slope ranged from approximately 12 to 17 cm long, with a mean of 15 cm. Sand lance schools observed on Stellwagen Bank were relatively large in numbers, ranging from about 500 to tens of thousands

[6]Boston Edison Company. 1974-77. Marine ecology studies related to operation of Pilgrim Station. Boston Edison Co., 800 Boylston Street, Boston, MA 02199.

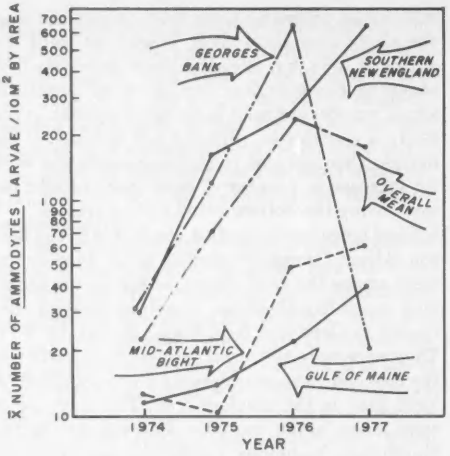

FIGURE 5.—Changes in the relative abundance of larval *Ammodytes* spp. in the Northeast Fisheries Center spring ichthyoplankton surveys from 1974 to 1977 in the area extending from Cape Hatteras northward. Data from Smith, W. G., and L. Sullivan. 1978. Annual changes in the distribution and abundance of sand lance, *Ammodytes* spp., on the northeastern continental shelf of the U.S. from the Gulf of Maine to Cape Hatteras. Northeast Fish. Cent., Sandy Hook Lab., Sandy Hook, NJ 07732. Lab. Ref. No. SHL 78-22.

of individuals. Individuals varied from 7.4 to 24.0 cm FL (measurements from bottom-trawl catches), with a mean length of 18.2 cm. Sand lance within a given school were of similar size; slightly larger fish were observed in positions at the head or central "core" of the school, with the smaller individuals occurring at the periphery. This distribution by size within the school was observed in both study areas. Schools were observed on the surface, at mid-depth, and near the bottom.

Inshore school strengths described by Kühlmann and Karst (1967) for European sand lance species *Hyperoplus lanceolatus* and *Ammodytes lancea* were commonly 30-100 or 200-300 individuals. These smaller schools joined up to form schools of from 500 to >1,000 fish and headed offshore for deeper water in the early morning. We observed schools of this size primarily in the Provincetown slope area. However, because the individual size of the fish and school strengths on Stellwagen Bank were larger, it is unlikely that these schools formed in the Provincetown slope area and moved out to the bank.

School Shape

The shape of sand lance schools, where individuals were not engaged in feeding, was constant in appearance. As a school moved undisturbed through the water it appeared vertically compressed, tightly compacted, and bluntly linear from the lateral view (Figure 6). Provincetown slope schools were 1-5 m wide, 0.5-1.5 m high, and 3-20 m long; these measurements depended on school strength. This school form, where the height-width-length ratio was approximately 1:3:10 (having more individuals situated ahead, alongside, and behind than above or below), is called a stratified school (Wahlert and Wahlert 1963). This school formation was, in general, independent of school strength. The "nearest-neighbor" distance between fish was approximately ½-¾ body length (BL) (Figure 6). This distance became greater along the school's flanks. The "nearest-neighbor" distance decreased to ¼ BL when the school exhibited a fright reaction to divers. The fishes leading the school and ones along the flanks usually swam the deepest. School shapes described by Kühlmann and Karst (1967) were similar to the measurements reported in this study, but a significant difference appeared in the school height and length measurements. Kühlmann and Karst (1967) listed their school height as 15-50 cm, and their school length as ≥40 m. Sand lance schools encountered in our study were more than double the height and shorter in length. The European study took place in water depths of 1-6 m, and in this relatively shallow water, there may be a tendency for a school to flatten out and increase its length.

Movement

The swimming motion of sand lance is sinusoidal in form and eellike in appearance from the dorsal and ventral views. Sidewise undulations begin at the head and run along the body toward the tail (Figure 7). Schools swimming undisturbed, and not engaged in feeding, maintain an estimated speed of 30-50 cm/s. Schools exhibiting feeding behavior usually swim at about half the speed of undisturbed schools, or about 15-25 cm/s, and spread out to a little over double the normal schooling distances so that the nearest neighbor is approximately 1-1½ BL away. Smaller schooling groups were observed to swim faster than larger schools. When approached by divers, schools ac-

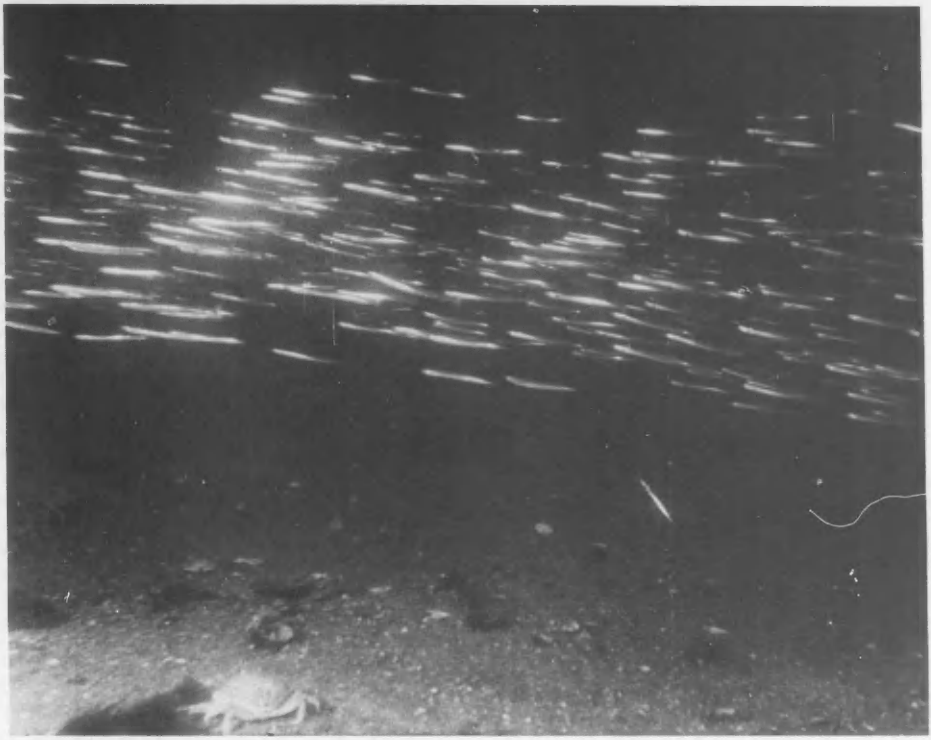

FIGURE 6.—School of sand lance encountered on Provincetown slope. Note lateral view of sand lance leaving the bottom to join school above.

celerated to one side or split to avoid the divers at the part of the school closest to the divers. The forward portion of the school continued on in its original direction, while the rear portion generally reversed direction. These avoidance maneuvers were made at about 70-120 cm/s, over double the original undisturbed speed, and lasted for only a few seconds before the divided sections regrouped and slowed down to their original speed. Feeding schools were observed in midwater and near the surface, but not on the bottom.

Kühlmann and Karst (1967) recorded the escape speed of larger sand lance to be 300-500 cm/s for at least a few seconds. During our study, there were many occasions when the swimming speed appeared to be >120 cm/s, but the actual speed was not calculated.

Behavior Within and Near the Ocean Floor

Sand lance were found in substrates conducive to burrowing, such as clean sandy bottoms, sand bottoms with crushed shells, and fine-graveled bottoms. Substrates of mud, mud/silt, medium to coarse gravel, and rock/boulder were avoided. This preference for loose porous substrate facilitates entry and exit and may relate to a sufficient supply of dissolved oxygen within at least the first few centimeters of interstitial water. Oxygen is continually replenished by tidal currents of 32-47 cm/s (0.62-0.91 kn) measured at 1 m above the bottom on Stellwagen Bank (Padan 1977).

Sand lance usually disappear into the bottom in small groups. The initial penetrating angle was estimated as 60°-75° from the horizontal and con-

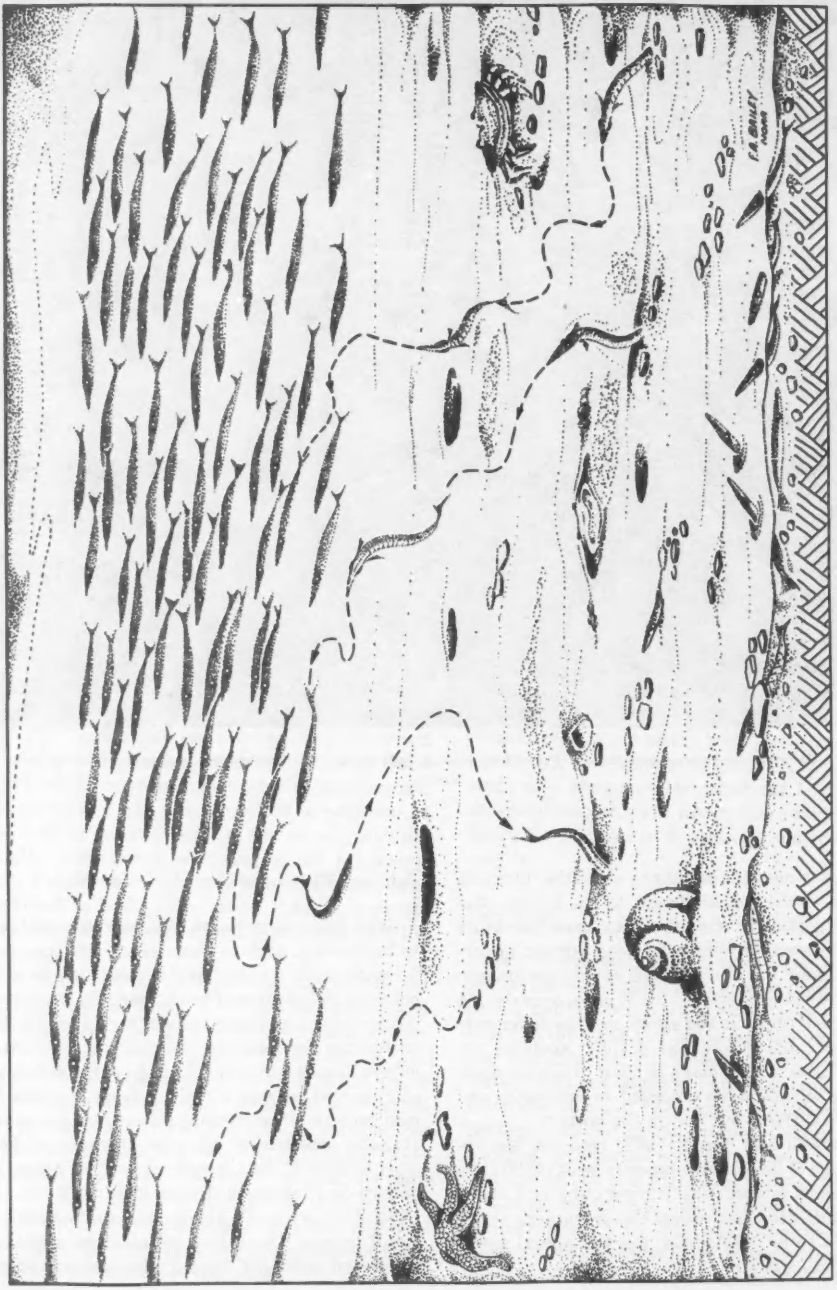

FIGURE 7.—Artist's rendition of sand lance behavior within and near the ocean floor.

sisted of a continuance of their sinuous movement until one-quarter of the body was buried, at which point the remaining three-quarters of the body was brought to a 20°-40° angle to allow the animal to settle into its normal resting position (Figure 7). Once in a resting position, the sand lance would partially emerge headfirst if disturbed (Figure 7). Sand lance on Stellwagen Bank, exhibiting this partial-emergence behavior, would retract back into the bottom when further disturbed. In contrast, sand lance encountered along Provincetown would usually leave the substrate. Kühlmann and Karst (1967) observed similar behavior and noted on several occasions that, after pulling back into the bottom, sand lance could turn, move laterally through the substrate, and emerge some distance away. This behavior was not observed in our study area.

Sand lance leaving the bottom exited at an angle between 20° and 60° with an initial speed of 50-80 cm/s, which increased up to 120 cm/s within the first 1.5 m from the bottom (Figure 7). As divers proceeded along the bottom, sand lance would exit from the substrate and either school or swim to the end of the diver's visual range.

Food Habits

The results of the stomach-content analysis for *A. americanus* collected on Stellwagen Bank are given in Table 2. The data are presented as both the percentage occurrence of prey in the stomachs and as the percentage weight of the total prey consumed. It is evident that copepods were the most important prey, occurring in 37.8% of the stomachs examined and making up 41.4% of the total weight of the prey. The other identifiable prey groups, such as hyperiid amphipods, mysids, euphausiids, chaetognaths, salps, and animal eggs, were much less important, usually occurring in only 1-2% of the stomachs. Of these groups only the chaetognath *Sagitta* contributed significantly to the diet on a percentage weight basis (39.9%). This was because the stomach of one fish was quite distended with chaetognaths. "Animal remains," which are unidentifiable prey, were the most frequently occurring prey category; however, on a weight basis they were much less significant.

The food habits of a number of different species of sand lance have been studied in Atlantic and Pacific waters. In general the diets are all very similar, with copepods being the major prey in almost every instance (Reay 1970). Around Japan,

TABLE 2.—Stomach contents of American sand lance collected on Stellwagen Bank, August 1977. The data are expressed as both the percentage frequency of occurrence of prey and as the percentage weight of the total quantity of prey consumed.

Prey	Occurrence (%)	Weight (%)
Copepods:		
Calanoida	3.3	0.81
Calanus	8.9	9.55
Centropages	10.0	2.57
Pseudocalanus	17.8	6.28
Temora	17.8	8.06
Tortanus	17.8	6.27
Metridia	1.1	1.22
Cyclopoida:		
Oithona	2.2	0.05
Unidentified	28.9	6.62
Copepod subtotal	37.8	41.43
Hyperiid amphipods	1.1	0.09
Mysids	1.1	0.32
Meganyctiphanes norvegica	1.1	0.41
Sagitta elegans	2.2	39.91
Salpidae	1.1	0.04
Animal eggs	1.1	<0.01
Trematodes	3.3	0.01
Animal remains	84.4	17.79
No. stomachs examined	90	
No. stomachs empty or trace	32	
Mean wt of contents/stomach	15.3 mg	
Mean fish length	18.2 cm, SD = 1.8	

for example, both Senta (1965) and Sekiguchi (1977) have shown that *A. personatus* is a plankton feeder relying heavily on copepods. In the North Sea, Roessingh[7] found that copepods were the major prey of *A. marinus* and occurred in roughly the same proportions in the stomachs as they did in the plankton. Macer (1966) examined the stomach contents of five species of sand lance from the North Sea. In all cases the sand lance were found to be plankton feeders, with copepods being the dominant prey for at least three of the five species. Only for *A. lanceolatus* was it conclusively shown that copepods were less significant as prey, being replaced by fish eggs, larvae, or small fish, particularly small *Ammodytes*. Two species of sand lance are reported to occur along the Atlantic coast of North America, and only a small amount of information is available on their food habits. Richards (1963) examined the stomachs of 290 *A. americanus* in Long Island Sound; as for most other species of sand lance, copepods were the major prey. *Centropages* were preyed upon by 80% of the fish, *Acartia* by 55%, and *Temora* by 42%. Other prey included barnacle cyprids, fish eggs, dinoflagellates and diatoms, mysids, and sand lance larvae. Scott (1973) studied the food habits of

[7]Roessingh, M. 1957. Problems arising from the expansion of the industrial fishery for the sand eel, *Ammodytes marinus* Raitt, towards the Dutch coastal area. Near Northern Seas Committee, Int. Counc. Explor. Sea.

A. dubius in the Canadian northwest Atlantic. Again, copepods, especially *Calanus finmarchicus*, were the most important prey. Other prey included crustacean larvae, invertebrate eggs, polychaete larvae, larvaceans, fish eggs, pteropods, and barnacle cyprids. Comparison with plankton tows made at the time the fish were caught showed that *A. dubius* had a definite preference for the larger zooplankton such as copepods. From the data in Table 2, it is clear that the diet of *A. americanus* from Stellwagen Bank is typical for this family of fishes. There are, however, several small differences from other published results which are worth noting. For example, chaetognaths occurred rarely in the stomachs (2.2%) but on a weight basis were only slightly less important than copepods. It would appear that chaetognaths are readily consumed if available. One notable exception to the list of prey is phytoplankton. Both Richards (1963) and Scott (1973), as well as Senta (1965) and Macer (1965), reported finding diatoms or dinoflagellates in the guts of the fish they examined. In our study, no phytoplankton was observed as part of the stomach contents. It is possible that at certain times of the year the occurrence of phytoplankton would be much more apparent in the guts, as might also be expected for other prey such as crustacean larvae, barnacle cyprids, and larval polychaetes.

SUMMARY

1. The meristic counts of sand lance reported are in agreement with published data and fall into the category of *Ammodytes americanus*, the American sand lance.

2. Data on the relative abundance of sand lance from Northeast Fisheries Center spring and fall bottom trawl survey cruises indicate that there has been a substantial increase in sand lance abundance on Stellwagen Bank over the last 10 yr. This trend was also reflected by an increase in the numbers of sand lance larvae occurring in the spring ichthyoplankton results measured in the Gulf of Maine over the last 4 yr. This increasing trend in larval and adult sand lance abundance in the Gulf of Maine was typical of the northwest Atlantic from Cape Hatteras northward.

3. Sand lance encountered within the Provincetown slope area ranged from 12 to 17 cm long (mean = 15 cm), and school strength numbered from about 100 to several thousand individuals. In contrast, individuals on Stellwagen Bank ranged from 7.4 to 24.0 cm FL (mean = 18.2 cm), while school strengths ranged from about 500 to tens of thousands of individuals.

4. School shapes were constant in appearance, vertically compressed, tightly compacted, and bluntly linear from a dorsal and ventral view. Provincetown slope schools were 1-5 m wide, 0.5-1.5 m high, and 3-20 m long depending on school strengths. The nearest-neighbor distance between fish swimming in an undisturbed school was approximately ½-¾ BL; between fish swimming in a school exhibiting a fright or avoidance reaction, ¼ BL; and between fish swimming in a school engaged in feeding, approximately 1-1½ BL.

5. The swimming motion of sand lance is sinusoidal in form and eellike in appearance. Schools swimming undisturbed and not engaged in feeding maintain an estimated swimming speed of 30-50 cm/s; during feeding they maintain an estimated speed of 15-25 cm/s; and during avoidance maneuvers, 70-120 cm/s. Feeding schools were observed in midwater and near the surface, but not on the bottom.

6. Sand lance were found to prefer clean sandy substrates conducive to burrowing. Sand lance usually disappear into the substrate in small groups, initially penetrating at an angle of 60°-75° from the horizontal, and continuing their sinuous movement until one-quarter of the body is buried, at which point the remaining three-quarters of the body is brought to a 20°-40° angle to allow the animal to settle into its resting position. Sand lance encountered on Stellwagen Bank were occasionally observed to partially emerge from the substrate headfirst and retract back into the bottom if approached. In contrast, sand lance along Provincetown slope would exit from the bottom when approached. Sand lance leaving the bottom exited at an angle of between 20° and 60° with an initial speed of 50-80 cm/s and built their speed up to 120 cm/s within the first 1.5 m from the bottom. Individual fish exiting would show schooling behavior if another fish was exiting at the same time.

7. Copepods were the most important prey of *A. americanus*, occurring in 38% of the stomachs examined and making up 41% of the total weight of prey consumed.

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SEASONAL DISPERSAL AND HABITAT SELECTION OF CUNNER, *TAUTOGOLABRUS ADSPERSUS*, AND YOUNG TAUTOG, *TAUTOGA ONITIS*, IN FIRE ISLAND INLET, LONG ISLAND, NEW YORK[1]

BORI L. OLLA, ALLEN J. BEJDA, AND A. DALE MARTIN[2]

ABSTRACT

Results of field observations examining seasonal movements in the cunner, *Tautogolabrus adspersus*, and young tautog, *Tautoga onitis*, showed a small portion of a resident population located off Fire Island, N.Y., to disperse seasonally. Dispersal was from habitats which provide cover for both species throughout the year to seasonal habitats occupied primarily during summer. While both species exhibit a high degree of association with cover, results of experimental transfers of young tautog, monitored either ultrasonically or directly by divers with self contained underwater breathing apparatus, showed that fish will leave a suboptimal habitat even though cover is present. Dispersal and habitat selection are discussed in relation to seasonal changes in the environment and ecological requirements of the fish.

Association with and dependence on cover by marine fishes have been observed for a wide variety of species, exemplified by those which reside on coral reefs (e.g., see: Hobson 1968, 1972, 1973; Sale 1969a, 1971, 1972, 1977; Smith and Tyler 1972, 1973). Although the number of species is much less, similar associations with cover also occur in temperate waters (e.g., see: Hobson 1971; Bray and Ebeling 1975; Hobson and Chess 1976; Olla et al. 1974, 1975).

In both tropical (Hobson 1968, 1972) and temperate regions a major behavioral trait of the family Labridae is that members show a strong association with cover. Field studies on two temperate-water labrids of the northwest Atlantic, cunner, *Tautogolabrus adspersus* (Olla et al. 1975), and young tautog, *Tautoga onitis* (Olla et al. 1974), have demonstrated their close association with cover. Under laboratory conditions similar associations have been observed for both species (cunner, Olla and Bejda unpubl. obs.; young tautog, Olla and Studholme 1975).

Over several years, incidental sightings of cunner and young tautog always found them in association with cover. However, it was apparent that a substantial number of fish were in areas in which cover was present only seasonally, e.g., macroalgae and mussel beds. This suggested to us that there must be movement to these areas sometime after emergence from winter torpor (Olla et al. 1974, 1975) in March or April and movement away from these areas in the fall as the cover provided at these areas diminished. The possibility of seasonal dispersal and habitat selection appeared likely. At least for adult tautog changes in habitat requirements with season have been established, as evidenced by the fact the fish migrate offshore to overwinter (Cooper 1966; Olla et al. 1974).

In this study we have examined seasonal movements in cunner and young tautog, basing our observations on trapping and tagging, as well as surveying shelter sites seasonally by direct observation with scuba or mask and snorkel. We also performed a series of transfer experiments to examine certain aspects of habitat selection.

MATERIALS AND METHODS

Based on previous scuba observations, six study sites (A, B, C, D, E, and F; Figure 1) within Fire Island Inlet, Long Island, N.Y., were selected at which to monitor the seasonal movements of cunner and young tautog. One site (A) was inhabited throughout the year and will be referred to as a perennial site. The five other sites (B, C, D, E, and F) were utilized only during late April through

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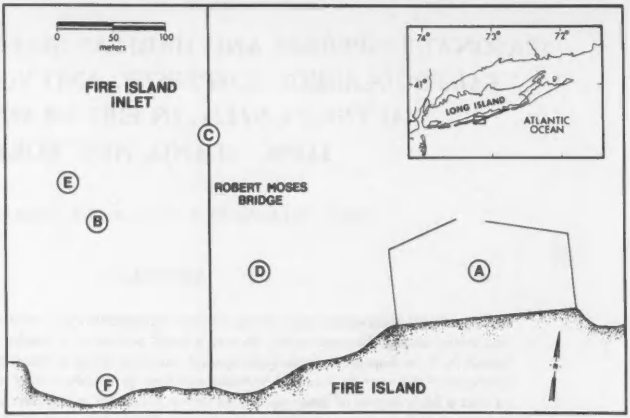

FIGURE 1.—Location of study sites for cunner and young tautog within Fire Island Inlet, Long Island, N.Y. (see text for site descriptions).

October and will be referred to as seasonal sites. A description of each site follows.

Site A was the boat basin at the Fire Island Coast Guard Station, an open pentagon (110 × 52 × 47 m), constructed of tongue-and-groove planks, steel sheeting, and piles (Olla et al. 1975). Along the outer perimeter was a zone of riprap (0.2– 0.4 m in diameter), 3 m wide and 2 m high. The mean water depth ranged from 2.4 to 8.8 m. Beds of the mussel, *Mytilus edulis*, were located along the walls, piles, and bottom.

Site B was a 20.3-cm diameter drain pipe originating at the Fire Island water treatment plant. Located at a mean depth of 7.5 m, a 1.5-m section of the pipe was exposed and paralleled the bottom at a distance of 1 m. Beds of mussels surrounded the pipe in about a 6-m radius.

Site C was one of the support piers for the Robert Moses Bridge, consisting of quarried stone and reinforced concrete. The mean water depth was 7.5 m. The pier was incrusted with mussels to a depth of 2 m below the high water mark.

Sites D and E each consisted of an exposed vertical mud bank about 6 m long and 1 m high. Irregularly spaced along the face of each bank were approximately 35 to 50 holes, apparently a result of erosion, varying in size from 12 to 20 cm wide and 5 to 15 cm deep. Small clumps of mussels were distributed along the top of each bank. Site D was at a mean depth of 6.0 m and Site E at 7.6 m.

Site F was a grass bed which bordered a rocky shore line for 75 m and extended out from the shore 13-20 m. During the late spring and summer, the area typically consisted of dense growths of eelgrass, *Zostera marina*, and algae (*Codium* spp., *Enteromorpha* spp., *Polysiphonia* spp., and *Ulva* spp.). Beds of mussels were interspersed between the vegetation. Water depth throughout the area varied from 0.3 to 1.5 m.

A seventh area, a small cove at the mouth of Fire Island Inlet, not designated in Figure 1, was the site of two transfer experiments involving experimental cover. This site had a barren sand bottom, primarily dredge spoil, at a mean depth of 3.7 m.

Three methods, trapping, direct visual counts, and tagging, were used to monitor, for both cunner and tautog, the periods and limits of movements as well as the types of habitats utilized. Fish traps were placed at Sites A, B, C, D, and E with two traps at Site A from March through November, one trap at Site B from May through November, and one trap each at Sites C, D, and E from June through November. Traps at each site were pulled at regular weekly intervals throughout the study and the number of cunner and tautog recorded. To compare the catch of the traps at the perennial site with the catch at the seasonal sites, we calculated the mean number of fish caught per trap per week for each habitat type. Traps captured cunner ranging in size from 3.9 to 25.0 cm ($\bar{x}$ = 14.5 cm) and tautog from 7.3 to 35.0 cm ($\bar{x}$ = 16.9 cm). Traps also provided the fish for the tagging portion of the study, as well as one means of recapture.

Visual counts of cunner and tautog were made at Site F from the end of February through October. A series of six transects the length of the site and 3 m wide were swum by divers, counting all

tautog and cunner observed within each transect with the sum of the six transects being the total count.

Cunner and tautog (≥14.0 cm) trapped at Sites A, B, C, D, and E were tagged throughout the study with Floy-67C[3]anchor tags. Tags were consecutively numbered allowing identification of individual fish and their release site. Each tag was printed with a request for fishermen catching tagged fish to return the tag, accompanied by information as to the location and date the fish was caught. Fish were recaptured either in our traps or by recreational fishermen.

Ultrasonic tracking was employed for short-term monitoring of movement and cover association of young tautog residing at both a perennial (Site A) and seasonal (Sites B and F) habitats. Four fish (two at Site A, one at Site B, and one at Site F) were individually tracked using the same procedures previously described by Olla et al. (1974, 1975) for capturing, handling, and tracking.

A series of transfer experiments was conducted to examine habitat selection in young tautog. All fish were captured at Site A and released at either existing, seasonal habitats (Sites B and C) or at experimental habitats which we established (see below). Fish were transferred by boat in 100-l barrels of aerated seawater with the time to travel from capture to release sites ranging from 5 to 15 min. Four fish (three at Site B and one at Site C) were separately released at the seasonal habitats and tracked ultrasonically. Five transfers were made to the experimental habitats. One transfer was a single fish, released and monitored ultrasonically. The other transfers consisted of four group releases with 10 fish/group. The response of the fish in these releases was monitored directly using scuba. While lying motionless, 5 m from the release site, the observer recorded at 1-min intervals the number of fish present. Cover at the experimental habitats consisted of masonry structures constructed from standard cement blocks (20 × 20 × 40 cm) positioned in a manner which laterally exposed the central cavities (7 × 13 × 20 cm) of each block. Cement blocks had been shown to be readily acceptable as cover by young tautog in the laboratory (Olla and Bejda unpubl. obs.). The structure for the single fish release was a four-block cube (40 × 40 × 40 cm). Two structures were used in the group releases. They were identical 12-block rectangular prisms (120 × 40 × 40 cm).

[3]Reference to trade names does not imply endorsement of commercial products by the National Marine Fisheries Service, NOAA.

RESULTS

Catch and Direct Sightings at Seasonal and Perennial Habitats

It was apparent from catch data and direct underwater sightings that a majority of the habitat sites were utilized only seasonally by both cunner and young tautog. Throughout the summer, substantial numbers of fish were captured at Sites A-E (Table 1) or sighted directly at Site F (Table 2). In September, there was a gradual decline in the catch of cunner and in October a sharp decline in both cunner and tautog at Sites B-E (Table 1). At Site F, direct visual counts indicated the same general trend (Table 2). However at Site A, while there was little change in catch during September, the catch of both species increased in October (Table 1). In November, Sites B-F were observed directly with scuba and no fish were sighted. At Site

TABLE 1.—Mean monthly catch of cunner and young tautog at perennial (A) and seasonal (B-E) sites.

	Mean catch/unit effort[1]			
	Cunner		Tautog	
Month	Perennial site	Seasonal sites	Perennial site	Seasonal sites
March	11.0	ND[2]	6.5	ND
April	36.0	ND	2.7	ND
May	6.8	9.5	2.5	9.2
June	19.7	8.5	1.3	10.6
July	13.8	5.3	0.6	11.9
August	21.8	6.1	6.2	9.8
September	21.9	2.8	8.6	8.0
October	34.0	3.0	14.9	1.0
November	9.7	0	3.8	0

[1]Unit effort = one trap fished 1 wk.
[2]ND = no data.

TABLE 2.—Visual counts using scuba or mask and snorkel of cunner and young tautog at seasonal Site F.

Date	Total number		Date	Total number	
	Cunner	Tautog		Cunner	Tautog
Feb. 28	0	0	July 2[1]	53	7
Mar. 4	0	0	8[2]	165	60
12	0	0	9[2]	93	27
20	0	0	10[2]	89	16
25	0	0	15	107	29
Apr. 2	0	0	16[2]	42	13
29	17	3	29	44	24
May 20	29	11	Aug. 12	63	20
22	74	20	13	169	71
29	60	15	Sept. 3	42	7
June 5	65	14	24	34	6
11	79	19	Oct. 2	0	0
18	10	0	20	0	0
26	69	12	29	0	0

[1]Mean of two counts.
[2]Mean of three counts.

A, although large numbers of fish were sighted, the catch was declining (Table 1). The decline in catch at Site A may be related to lowered activity associated with decreasing temperature with the fish overwintering in torpor at this site (Olla et al. 1974, 1975). Although traps were not in place in Sites B-E earlier than May, no fish were sighted directly in these areas or at Site F (Table 2) prior to mid- or late April. The presence of fish at Site A throughout the year led us to term this a perennial habitat, while Sites B-F, where fish were only seen seasonally, we defined as seasonal habitats.

Recaptures

Tagged fish showed limited movements, with 91.3% of the cunner and 73.2% of the tautog recaptures occurring at the same site at which they were released (Table 3). For the remainder of the fish, i.e., those recaptured at other sites, there were seasonal differences in where they were captured. From May through August, recaptures were at seasonal as well as perennial sites (Table 3). But then from September through November, all recaptures were from sites which would be considered perennial, including ones outside the study area (Table 3).

Movements and Association with Cover of Young Tautog at Seasonal, Perennial, and Experimental Habitats

In an earlier study, we had established that young tautog remained within several meters of cover (Olla et al. 1974). Specifically, the cover referred to in that study was Site A, identified in this study as a perennial habitat. To reconfirm the observation of the previous study, two fish (no. 1, 2; Table 4) were ultrasonically tracked for 48 h at Site A. Agreeing with the earlier results, both fish remained within several meters of the site.

The question we next addressed was whether young tautog showed a similar association with cover at seasonal habitats. To answer this question, we captured and released two fish affixed with ultrasonic tags at Sites B (no. 4; Table 4) and F (no. 3; Table 4). The results of tracking showed the two fish to have a similar affinity to these sites as the fish had to the perennial one, remaining within 3 to 6 m of cover.

The area over which the fish ranged varied with the size of the site. For example, when fish no. 3 was released at Site F, which consisted of beds of algae and eelgrass measuring about 15 × 75 m, it moved freely throughout the habitat, but never more than several meters beyond its perimeter. On the other hand, fish no. 4 released at Site B where cover was highly limited (0.2 × 1.5 m) exhibited less movement, while again remaining within several meters of cover. It appeared that the close association to cover was the same at both seasonal and perennial habitats.

Thus far, all of the fish that were tracked had been released at the same site at which they were captured. Our next question was whether fish that were displaced from where they were captured

TABLE 4.—Size, capture and release sites (Figure 1), and period monitored for nine young tautog ultrasonically tracked.

Number	TL (cm)	Capture site	Release site	Tracking duration (h)
1	22.5	A	A	48
2	24.0	A	A	48
3	20.2	F	F	24
4	24.5	B	B	48
5	21.5	A	B	48
6	22.8	A	B	72
7	23.0	A	B	48
8	24.0	A	C	48
9	22.5	A	[1]	24

[1]Experimental cover.

TABLE 3.—Number and location of recaptures of cunner and young tautog tagged and released at perennial and seasonal sites.

Species	Release site	No. released	Total no. recaptured	No. recaptured at release site	No. recaptured at other sites: May-August, Perennial sites	May-August, Seasonal sites	September-November, Perennial sites	September-November, Seasonal sites
Cunner	A	875	176	166	5	1	4	0
	B	83	13	7	0	3	3	0
	C	15	0	0	0	0	0	0
	D	54	6	5	0	0	1	0
	E	10	0	0	0	0	0	0
	Total	1,037	195	178	5	4	8	0
Tautog	A	245	25	20	0	1	4	0
	B	283	29	18	0	5	6	0
	C	72	12	11	0	0	1	0
	D	123	3	2	0	0	1	0
	E	41	2	1	0	1	0	0
	Total	764	71	52	0	7	12	0

would accept and remain at a different site. Four fish captured at Site A, the perennial habitat, were affixed with ultrasonic tags and released at either of two seasonal sites. Three fish were released separately at Site B (no. 5-7; Table 4) and a fourth at Site C (no. 8; Table 4) and individually tracked for 48 to 72 h. The fish appeared to accept the transfer to a different habitat with all four fish remaining within several meters of the release site.

The close association with cover exhibited by fish ultrasonically monitored at both perennial and seasonal habitats indicated the possibility that the apparent dependence on cover might be such that a fish would remain at any object that afforded cover. To examine whether the presence of cover was the sole determinant of habitat acceptance, we transferred a fish from Site A to a structure constructed of cement blocks, measuring 40 × 40 × 40 cm, and located on a sand bottom 50 m from a habitat with which fish were associated (Site F). The fish (no. 9; Table 4), during the first 5 min after release, circled the structure and moved farther away with each circuit, showing little, if any, attraction. When about 10 m from the structure, it swam shoreward and reached Site F about 5 min later. The fish remained at this site during the next 24 h, showing the same degree of movement exhibited by fish no. 3 (Table 4) which had been previously captured and released at this site.

It was possible that the fish moved from the structure because of its proximity to a natural habitat, therefore affording it a choice. It was also possible that social factors related to the release of a single fish rather than a group may have played a role in the rejection of the structure as a habitat. To control for these factors, we next released fish in a group of 10, 4.5 km from their home range and 100 m from the nearest natural habitat at which conspecifics were present. To broaden the scope of our queries we included the possible influence of factors such as food and naturally occurring cover on habitat selection. Two cement block structures (120 × 40 × 40 cm) were placed 10 m apart. Both were identical except that while one consisted simply of bare cement blocks, the other contained clumps of mussels and algae (*Ulva* sp.), naturally occurring food and shelter material. Two groups of 10 fish each (15-23 cm) captured at Site A, were released together at each habitat while being observed with scuba. Within 5 min of being released, the fish left both structures, swimming away in various directions.

The habitats were then modified by the addition to each of a fish trap. To the habitat which contained mussels and algae the trap added was overgrown with various fouling organisms and had been in continuous use over a period of 4 to 5 mo, capturing both tautog and cunner. The fact that this trap captured fish consistently led us to conclude that it provided an attractive stimulus or set of stimuli. The trap added to the bare structure was new. A group of 10 fish (10-25 cm), captured at Site A, was released at each habitat. As previously, the fish left the bare habitat within 5 min. Dispersal from the other habitat was more gradual with the last fish leaving about 60 min after release. In all instances, the fish departed, indicating that factors in addition to those provided were necessary for mediating habitat selection.

DISCUSSION

It was clear from the results of trapping, tagging, and direct underwater observation that some portion of the cunner and young tautog populations dispersed in late spring. The dispersal was from the boat basin (Site A, which we termed a perennial habitat) to habitats that were utilized only seasonally. Once adopting a seasonal habitat, the fish appeared to remain there until fall. Then there was a general movement back to a perennial habitat, but as was evident from the capture of tagged fish at perennial sites outside of the study area, not necessarily the one from which they dispersed in the spring. Once arriving at a perennial habitat, the fish remained to overwinter in torpor, not emerging until sometime in early spring when the temperature reached 5° to 6°C (Olla et al. 1974, 1975).

Supporting our findings for seasonal movement, Briggs (1977) found a marked increase in the number of young tautog captured during the fall at the Kismet artificial reef, 6 km from our study area. This increase, we surmise, also reflects the movement of fish from seasonal habitats to one which appears to be perennial.

In attempting to define habitat requirements for both species, it is apparent that cover is a critical factor. During the day when these fish are active, they remain within several meters of cover, and at night when quiescent and unresponsive, they are either in, against, or under cover (Olla et al. 1974, 1975). Once becoming torpid in winter, they remain under cover until spring. It seems reason-

able to assume that dependence on cover is related to protection from predation. Large adult tautog, not as vulnerable to predation because of their size, move away sometimes considerable distances from cover each day to feed (Olla et al. 1974).

With such a strong tendency to remain in proximity to cover, the question arises as to what causes a portion of the population to disperse. It is clear that environmental factors are changing with season as are the requirements of the fish. Both species in the spring have emerged from 3 to 4 mo of torpor, which has required them to live on stored energy reserves. The need for food arising from winter deprivation, coupled with the increased metabolic requirements resulting from the increase of temperature in late spring, might stimulate feeding and the competition for food. At least until June, the major dietary component for both species is *Mytilus edulis* (Olla et al. 1975), and thus competition for food would be both intra- and interspecific.

The spawning season for cunner also peaks during June (Dew 1976). Thus we can expect that competition for participation in either group spawning (Wicklund 1970) or pair spawning (Pottle and Green[4]) would increase. This increase would relate either to participation in gamete release or male territoriality as related to pair spawning. Although the majority of tautog studied were immature and would generally not be involved in the reproductive competition, it is possible that the arrival from offshore of adults that are in spawning condition (Olla et al. 1974) and which we know to be highly aggressive (Olla and Samet 1977; Olla et al. 1977) may also play a role in the dispersal of the smaller fish.

Competition in both species is manifested through aggression (for tautog, Olla and Studholme 1975; Olla et al. 1977, 1978; for cunner, Olla and Bejda unpubl. field and laboratory obs.). The increase in aggression that may occur at the perennial habitat as a result of competition could cause this site to become suboptimal, at least for some portion of the population. Seasonal changes in levels of aggression within a population might result in corresponding seasonal changes in the carrying capacity of the habitat.

Support for the idea that fish will leave a suboptimal habitat is reflected in the results of the transfer experiments where young tautog left the cement block structures provided for them. Similar results were obtained with juvenile cunner (Olla unpubl. obs.). In attempting to examine the mechanism for habitat selection in the manini, *Acanthurus triostegus sandvicensis*, Sale (1969b) performed a series of laboratory experiments and concluded from these that there was a higher intensity of exploratory behavior exhibited when animals were subjected to an inadequate environment. Similarly, it could be concluded that young tautog were showing greater exploratory behavior when they left the experimental cover provided for them. A portion of the fish that disperse will be lost, with the probability of survival decreasing as the amount of time taken to find a suitable habitat increases. Nevertheless, through this mechanism, fish are able to utilize seasonally available resources.

The return to perennial habitats from seasonal ones in the fall may also be related to these becoming suboptimal for the fish, but for different reasons than those which caused dispersal in the spring. At habitats which exist only seasonally, as in the case with macroalgae and eelgrass beds, the actual cover that these beds provide begins to wane as they start to die back in the fall. Although some sites were structurally more permanent, such as Site B (the submerged pipe), the animals did not use them as perennial habitats, and the changes which were occurring to render them suboptimal were not obvious. Besides changes in the environment, of prime importance for consideration is the change in the animals' requirements for cover. What served adequately in summer is not adequate for winter.

In observing cunner and young tautog in the field during winter torpor, both species were found in deep recesses and often buried under several millimeters of sand, farther under cover than observed during nighttime quiescence in summer. This afforded them greater protection during the winter. The seasonal sites studied did not provide cover equivalent to that at perennial ones, which have numerous deep crevices and holes.

Laboratory studies on adult tautog confirm the change in cover requirements during winter torpor (Olla et al. 1977; Olla and Studholme 1978). As temperature declined, the fish began to show an affinity for those structures which would serve as cover during the winter at least 1 to 2 wk before

[4]Pottle, R. A., and J. M. Green. 1978. Field observations on the reproductive behaviour of the cunner, *Tautogolabrus adspersus* (Walbaum), in Newfoundland. Unpubl. manuscr., 27 p. Department of Biology and Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Newfoundland A13 3X9.

torpor was observed at which time the fish actually burrowed under them being almost completely covered by sand. These structures differed from the ones the fish used throughout the rest of the year at night. In the field, the offshore movement of the adults begins 4 to 8 wk before they would encounter temperatures that would induce torpor (Olla et al. 1974), indicating a change in habitat requirements with season. About the same time that adult tautog are moving offshore, cunner and young tautog are moving to perennial sites.

Association with cover is no doubt a strongly motivated behavior for young tautog and cunner, but one for which there is a considerable range of adaptation. Under seasonally changing conditions or when habitats are simply suboptimal as in the transfer experiments, the animals will disperse, leaving cover at the risk of predation until alternate sites are found (as discussed earlier). On the other hand, a closer association results from transient environmental causes, such as the presence of predators resulting in young tautog fleeing to cover (Olla et al. 1974). Similarly, elevated temperature stress causes young tautog to associate more closely with cover, at least under laboratory conditions (Olla and Studholme 1975).

ACKNOWLEDGMENTS

We wish to thank the personnel of the U.S. Coast Guard, Fire Island Station, N.Y., for their assistance and cooperation.

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BIOLOGY OF WALLEYE POLLOCK, *THERAGA CHALCOGRAMMA*, IN THE WESTERN GULF OF ALASKA, 1973-75

STEVEN E. HUGHES AND GEORGE HIRSCHHORN[1]

ABSTRACT

Data on the stock composition, growth, mortality, and abundance of walleye or Alaska pollock, *Theragra chalcogramma*, in the western Gulf of Alaska were collected during six demersal trawl surveys in 1973-75. Over 102,000 km² of continental shelf and slope were surveyed; most of this area was covered during spring and summer.

Using the area-swept technique and catchability coefficients of 1.0 and 0.5, the exploitable pollock biomass in the survey region was between 610,000 and 1,220,000 metric tons. The percentage of larger and older fish increased to the west. Sexual maturity was reached at age 3. Growth completion rates ranged from 0.2 to 0.4. Natural mortality was estimated (assuming natural mortality equals growth completion rate) at 0.33 for males and 0.30 for females. Variations in growth completion rates within year class and variable recruitment strength indicated a probable east-west separation of pollock spawning populations near Kodiak.

The National Marine Fisheries Service conducted six trawl surveys of walleye or Alaska pollock, *Theragra chalcogramma*, and other groundfish resources in the western Gulf of Alaska from Cape Cleare, Montague Island, west to Unalaska Island during each spring and summer of 1973-75 (Figure 1). These surveys have provided information on the geographic and bathymetric distribution and densities of species within the groundfish commmunity (Hughes and Parks 1975).

An additional goal of these surveys and subject of this report was the collection of pollock life history data for management purposes.

METHODS

Six cruises were completed. Five were conducted from the 28-m NOAA RV *John N. Cobb*, employing 400-mesh Eastern otter trawls with 30-m footropes. During these five surveys, fishing was conducted following a predetermined, stratified random survey pattern (Grosslein[2]). Fishing densities varied from one 30-min trawl/1,370 km² in strata of anticipated low densities (depths of 90 m or less) to one 30-min trawl/515 km² in the remaining depth strata of 91-180 m, 181-270 m, 271-360 m, and 361-450 m. The other cruise was conducted from the 26-m chartered trawler *Anna Marie*, with similar but larger modified Eastern and Norwegian-style otter trawls with about 34-m footropes. Because the purpose of the *Anna Marie* survey was to determine commercial production potentials (Hughes and Parks 1975), fishing was concentrated where fish schools were detected by echo sounding; no predetermined survey pattern was followed. Consequently, the *Anna Marie* data (Sanak-Unalaska, May-June 1974) were not used for pollock density or biomass studies.

Stretch mesh measurements (1 knot included) of all trawls ranged from 10.2- to 14.0-cm mesh in the intermediate and cod end sections. Trawls measured by scuba divers at depths of 15 m indicated vertical heights of 2-3 m and horizontal spread of 11-13 m.

Methods of selecting random samples of pollock for collection of biological data were consistent during all surveys (Hughes 1976a). Length-frequency fork length (FL) measurements to the nearest centimeter by sex were randomly collected from each catch with the desired sample size being 300 pollock. While processing pollock for length-frequency data, stratified subsamples of otoliths (10/sex per cm) and individual fish weights (5/sex per cm) were taken (±5 g). Otoliths were stored in ethanol in plastic boxes (Hughes 1976b) and ages were later determined as described by LaLanne (in press).

Length-frequency distributions determined

[1]Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Grosslein, M. D. 1969. Some observations on accuracy of abundance indices derived from research vessel surveys. Unpubl. manuscr. Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

Manuscript accepted August 1978.
FISHERY BULLETIN: VOL. 77, NO. 1, 1979.

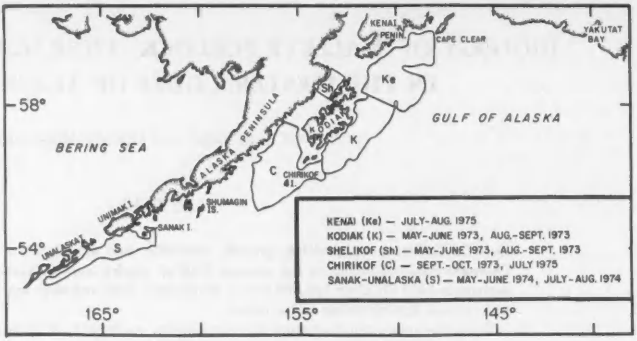

FIGURE 1.—Western Gulf of Alaska regions where trawl surveys were completed, 1973-75.

from the five standard resource assessment surveys were weighted by catch magnitude and area within sampling strata, whereas data collected during the commercial fishing (Sanak-Unalaska, May-June 1974) trials were weighted only by catch magnitudes. Length-age data from the stratified otolith collections of sexed pollock in each survey region (Figure 1) were compiled into age-length keys.

The proportions of observed ages on each length interval above 19 cm were applied to the weighted length frequencies. For this we used a computer program by Allen (1966) modified to exclude extrapolations beyond the aged length range and to include the calculation of mean length at age, as well as numbers at age. Thus numbers and size of pollock in the fishable population were estimated by region, age, and sex.

Resulting analysis provided weighted age composition data and mean length-at-age data for growth studies. Von Bertalanffy growth-in-length parameters and length-weight data were determined for each region.

An area-swept technique (Alverson and Pereyra 1969) was employed to estimate the pollock exploitable biomass, using the relation $\bar{P}w = (\text{CPUE})\,(A)/(c)\,(\bar{a})$ where $\bar{P}w$ is equal to the average standing stock, in weight, of the catchable population. A is the total area; $\bar{a}$ is the average bottom area covered by the trawl per standard tow; and c is a coefficient related to the effectiveness of the trawl in capturing pollock.

Whereas earlier studies of Alaskan pollock assumed $c = 1.0$ (Alverson and Pereyra 1969), pollock were often acoustically detected off the sea bottom and above the trawl's headrope. Estimates of c given for some gadoid species of the northeastern Atlantic Ocean indicated c may not exceed 0.51 (Edwards 1968). In this report, values of both 0.5 and 1.0 provide a conservative range of biomass estimates.

RESULTS

The surveys resulted in 144 fishing days on the grounds and 368 successful trawl hauls. Over 455,000 kg of groundfish were sampled, including 49,912 pollock which were processed for biological data.

Size and Age Composition

In the three regions where spring and summer surveys were conducted during the same year (Shelikof Strait 1973; southeast Kodiak 1973; and Sanak-Unalaska 1974), seasonal variations in size and age composition were attributed to fish measuring <28 cm which represented the 1- and 2-yr-old juvenile segment of the population (Figures 2, 3). However, substantial differences between regions indicate that size and age of adult pollock consistently increased when moving from the southeast Kodiak and Shelikof Strait regions westward through the Chirikof region and into the Sanak-Unalaska region.

The age composition data also indicated that Gulf of Alaska pollock display strong variations in year-class strength. Both 1967 and 1970 year classes showed unusually strong recruitment. Indication of a strong 1967 year class, sampled as 6-yr-olds, was noted during the May-June 1973 surveys of the southeast Kodiak and Shelikof regions. The relative strength of this year class was again noted 3 mo later during the August-September survey of southeast Kodiak and, particularly, of Shelikof Strait. Farther west, in the October 1973 Chirikof

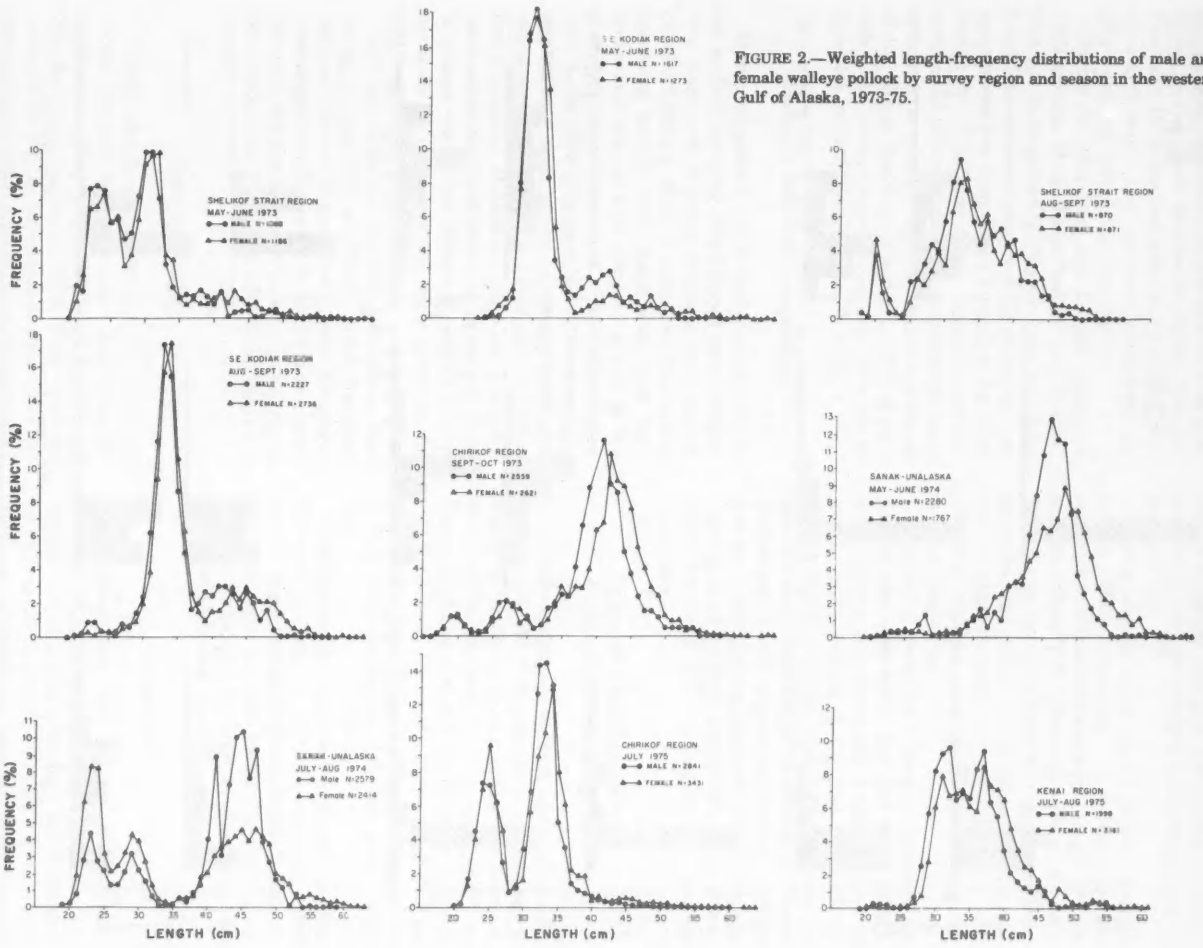

FIGURE 2.—Weighted length-frequency distributions of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75.

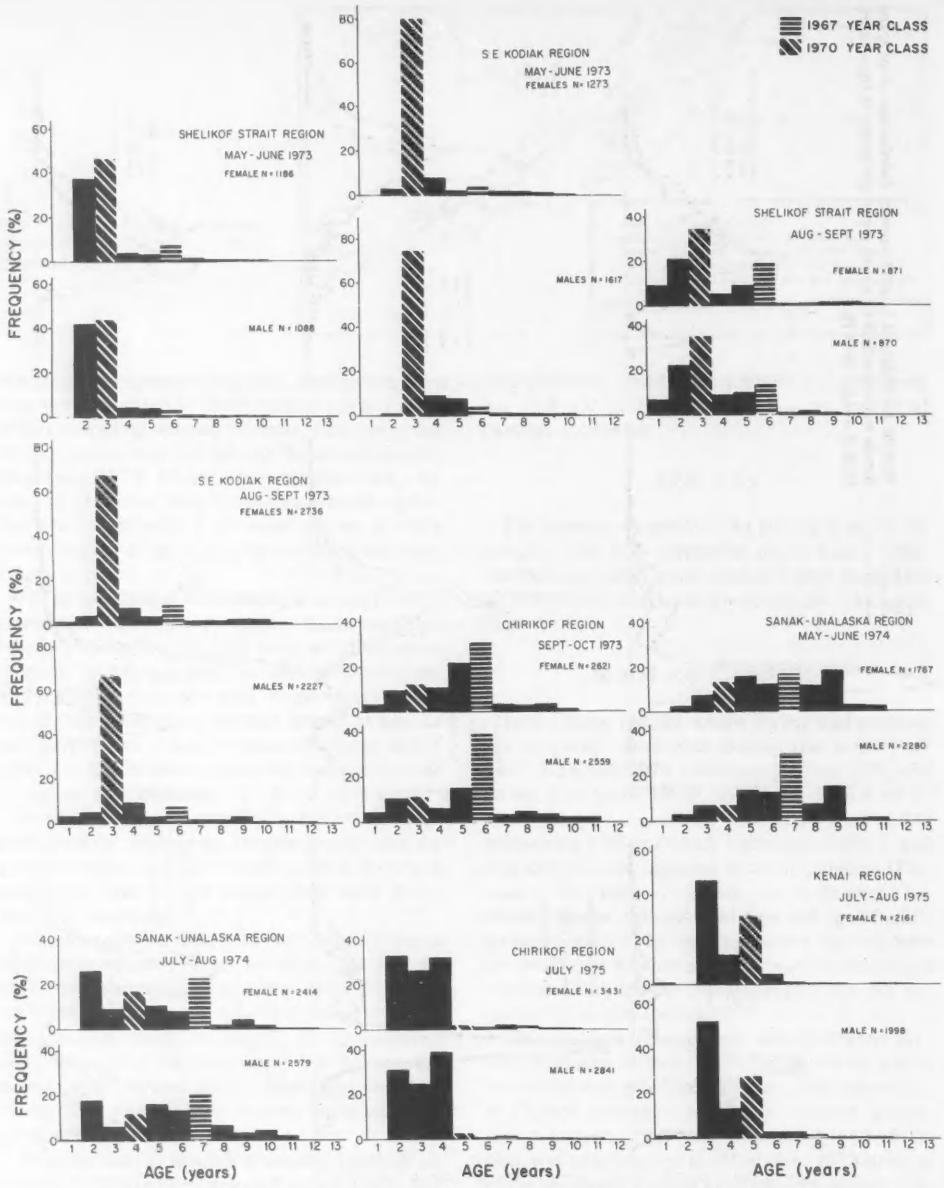

FIGURE 3.—Weighted age-frequency distributions of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75.

survey, 6-yr-old pollock were dominant. One year later, in the most westward region (Sanak-Unalaska 1974), the prominence of the 1967 year class as 7-yr-olds was apparent during both the May-June and July-August surveys.

During the May-June and August-September 1973 surveys of southeast Kodiak and Shelikof Strait, 3-yr-old pollock (1970 year class) were dominant. The unusual strength of this year class was again noted 2 yr later east of Kodiak as 5-yr-olds during the 1975 Kenai survey. However, recruitment of the 1970 year class was not successful west of Kodiak, as shown by the low relative abundance of 3-yr-olds in the Chirikof region in 1973, of 4-yr-olds in the Sanak-Unalaska region in 1974, and of 5-yr-olds in the Chirikof region in 1975.

Maturity and Sex Composition

Most adult pollock (>85%) had spawned prior to our earliest sampling (May). Based upon a subjective evaluation of gonad condition from pollock collected during May, it appeared that prime spawning periods were March and April. Ripe males and females were obtained as late as August, but these represented <0.1% of samples. Both sexes were fully recruited to the spawning population at age 3. Mature or recently spent age 2 males were encountered but represented <5% of that age-group. Mature or spent age 2 females were not encountered; however, minor gonad enlargement was noted. Means of lengths at first maturity in spring surveys were 29-32 cm for males and 30-35 cm for females.

Our data indicate that sex composition fluctuates around 50% at 20-45 cm FL but that females become progressively more dominant with larger size (Figure 4). As will be shown later, the point of major difference in sex ratio (45 cm) is composed primarily of age 4, 5 females and age 5, 6 males.

Length-Weight

Pollock length-weight data by sex were collected during the May-June and August-September surveys of the southeast Kodiak and Shelikof Strait regions in 1973. Data were also collected during the September-October 1973 survey of the Chirikof region. Length-weight relations were determined for these survey regions and periods (Figure 5) by fitting the logarithmic form of the equation ($W = aL^d$). where W is body weight in grams and L is fork length in centimeters, to the mean weight per centimeter-length interval.

Comparison of these curves indicates that female pollock measuring >33 cm weighed considerably less than males of equal length during the May-June postspawning survey. Female weight gain during summer was more rapid than in males, and differences in weight-at-length in the Shelikof Strait, southeast Kodiak, and Chirikof regions were negligible during the August-October sampling.

Regional differences during spring-summer periods were also noted. Shelikof Strait pollock were heavier than southeast Kodiak pollock of equal length during spring and considerably lighter during summer. This difference may be due to a more rapid weight gain in the southeast Kodiak region or to migration of the most healthy fish out of Shelikof. An additional factor suggesting migration was that samples of male pollock in Shelikof actually showed a weight loss from spring to summer.

Density Distribution and Estimates of Standing Stock

Pollock were distributed over depth intervals of 50-360 m (Table 1). Highest densities occurred at depths of 91-270 m during spring and summer. Geographically, densities were highest at Sanak-Unalaska (181-270 m), followed by southeast Kodiak (91-180 m). Spring-summer 1973 assessment surveys of Shelikof Strait and southeast Kodiak indicated highest densities during summer.

The summer biomass of pollock exceeding 20 cm FL was estimated as 610,000-1,200,000 metric tons (t) of whole fish (Table 1). Regional biomass estimates were greatest in the Chirikof region, followed by Sanak-Unalaska, southeast Kodiak, Kenai, and Shelikof Strait.

Growth

Length-age data from the nine surveys were fitted by the von Bertalanffy relation $l_t = L_\infty \{1 - \exp k(t-t_0)\}$ following computational procedures by Fabens (1965). Because variation in age range affects comparability of parameters (Hirschhorn 1974), curve fits over original age ranges were supplemented: 1) with fits over a standardized age range of 2-8 yr, 2) with an artificial data point (0,0)

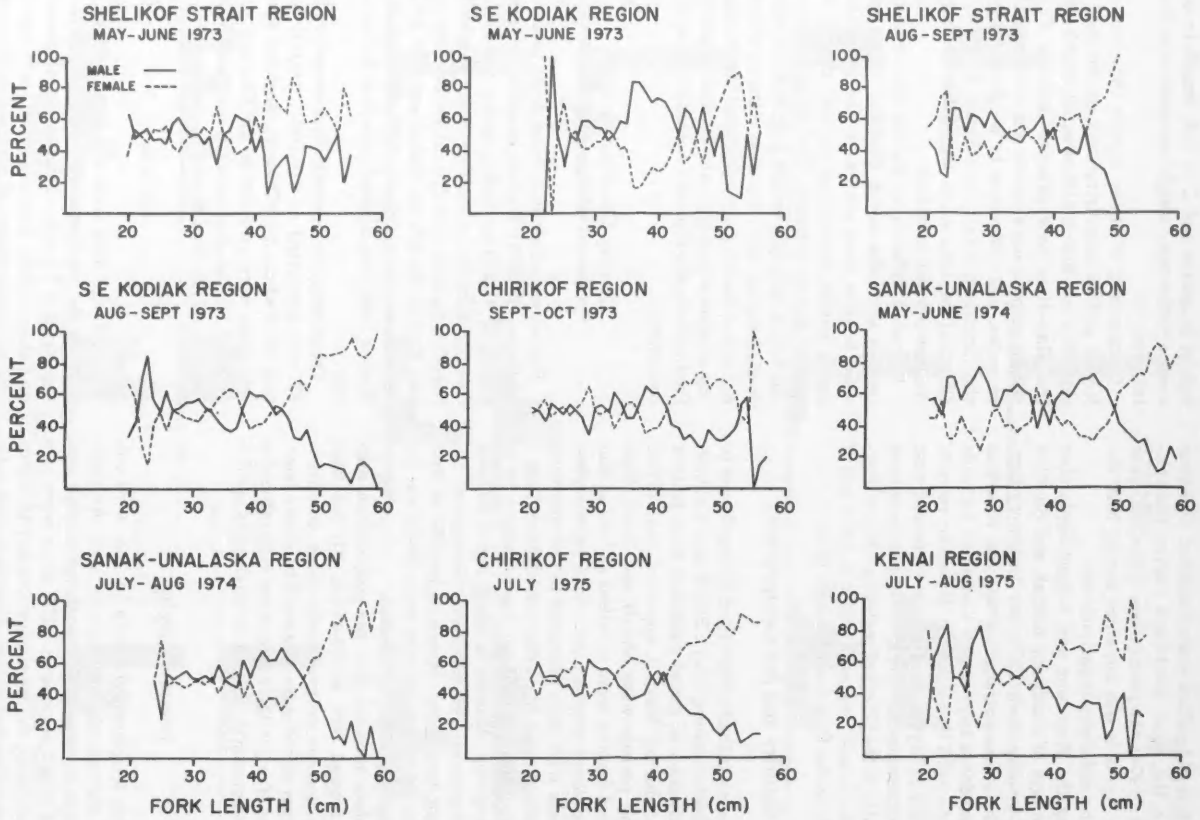

FIGURE 4.—Walleye pollock sex composition plotted as a function of increasing fish length by survey region and season in the western Gulf of Alaska, 1973-75.

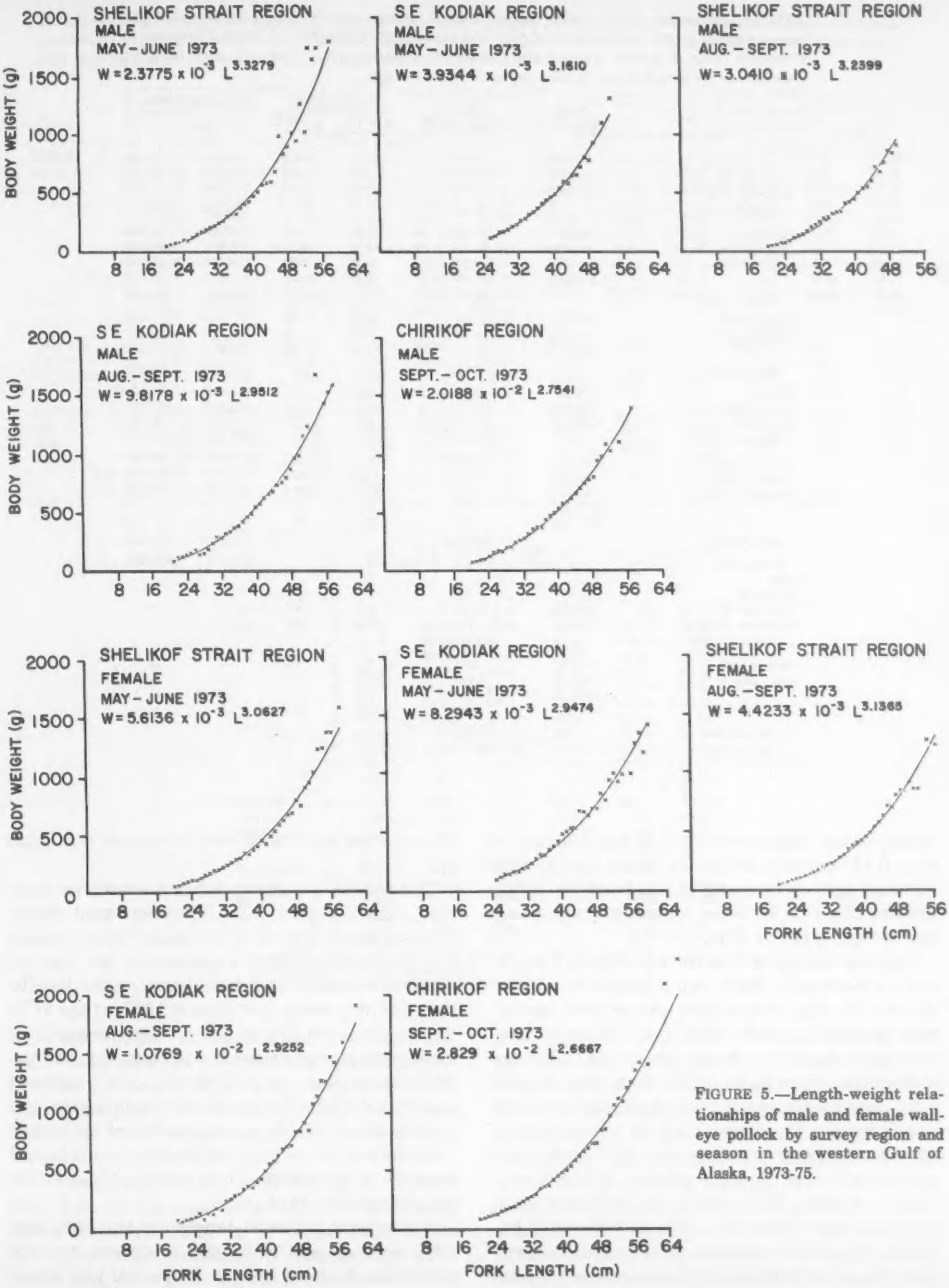

FIGURE 5.—Length-weight relationships of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75.

TABLE 1.—Summary of exploitable walleye pollock biomass and density by depth strata and survey regions in the western Gulf of Alaska. Catchability coefficients 1.0 and 0.5 are used to produce a range of pollock biomass and density. Biomass estimates were calculated from the summer survey period due to limited spring survey coverage.

Survey region and period	Depth strata (m)	Area surveyed (km²)	Density (t/km²)		Exploitable biomass (t)	
			c = 1.0	c = 0.5	c = 1.0	c = 0.5
Summer:						
Kenai Peninsula	91-180	19,183	4.1	8.2	77,742	155,485
(148°-152°W)	181-270	8,026	2.8	5.6	22,230	44,460
July-Aug 1975	271-360	796	0.2	0.4	186	371
Regional total		28,005			100,158	200,316
SE Kodiak	55-90	7,302	2.2	4.4	16,180	32,360
(152°-154°W)	91-180	6,143	16.1	32.2	99,042	198,085
Aug-Sep 1973	181-270	1,475	9.9	19.8	14,706	29,412
	271-360	737	0	0	0	0
Regional total		15,657			129,928	259,857
Shelikof Strait	55-90	381	0.2	0.4	89	178
(Aug-Sep 1973)	91-180	3,341	5.8	11.6	19,480	38,960
	181-270	2,713	1.0	2.0	2,610	5,221
Regional total		6,435			22,179	44,359
Chirikof	55-90	9,439	1.0	2.0	9,082	18,163
(154°-159°W)	91-180	12,749	13.6	27.2	173,583	347,168
July 1975	181-270	11,661	0.2	0.4	11,220	22,440
Regional total		33,849			193,885	387,771
Sanak-Unalaska	50-90	6,547	2.7	5.4	18,060	36,120
(162°-168°W)	91-180	8,935	13.1	26.2	117,096	234,192
July-Aug 1974	181-270	912	31.8	63.6	29,107	58,214
	271-360	703	0	0	0	0
	361-450	322	0	0	0	0
Regional total		17,519			164,263	328,526
Survey total		101,465			610,413	1,220,826
Spring:						
SE Kodiak	50-90	4,778	0.4	0.8	—	—
(148°-152°W)	91-180	4,496	2.0	4.0	—	—
May-June 1973	181-270	737	0.4	0.8	—	—
Regional total		10,011				
Shelikof Strait	50-90	381	0.2	0.4	—	—
(May-June 1973)	91-180	3,982	0.7	1.4	—	—
	181-270	11,558	0.6	1.2	—	—
	271-360	1,008	0.3	0.6	—	—
Regional total		16,929				
Survey total		26,940				

added on the assumption that at age 0 length is near 0 (Alverson and Carney 1975), and 3) with nominal ages or ring counts incremented by the fraction of a year between middates of spawning and sampling (Δt in Table 2).

Because each growth pattern in Figure 6 represents a synthetic cohort, i.e., a composite of year classes, the departures from the pattern, generated by members of the 1967 and 1970 year classes, were examined in detail. According to the age composition discussed earlier, both year classes were encountered in relatively high abundance at one extreme of the survey range (Figure 3) and in low abundance at the other (the 1967 year class was prominent at Sanak-Unalaska, the 1970 year class at Kenai). To examine the evidence for a growth-density relation, the size differences between the synthetic growth curves and observed mean lengths of the sampled age-groups of these year classes were calculated (lower part of Table 2).

The results are shown along a schematic east-west axis in Figure 7. In the easternmost region (Kenai), the strong 1970 year class indicates negative departures from expectation (at age 5), whereas corresponding departures are positive for the relatively weak year class of 1967 (at age 8). In the westernmost region, the relative strengths of these year classes seemed to be reversed, and the direction of departures of their mean lengths at ages 4 and 7 also reversed. By this criterion, the segregation of the two components of each year class was most pronounced at the extremes and least so in the intermediate Kodiak-Shelikof region where the lines cross.

Age-specific observed lengths of the 1970 and 1967 year classes were also compared directly with those of others, apparently weaker year class-

TABLE 2.—Mean length (centimeters) at age of western Gulf of Alaska *Theraga chalcogramma* by survey and sex; growth parameters (L_∞, K, t_0) for original and "selected" data sets, with standard deviation (σ) of departures from fit; departures of 1967 and 1970 year class mean lengths at age, from fit (Δ67YC, Δ70YC).

		Sanak				Chirikof				Kodiak			
		May-June 74		July-Aug. 74		July 1975		Sept.-Oct. 73		May-June 73		Aug.-Sept. 73	
Item		M	F	M	F	M	F	M	F	M	F	M	F
		(0.17)[1]		(0.42)		(0.25)		(0.50)		(0.17)		(0.42)	
Years of age (t)	1	—	—	20.00	—	—		19.49	20.02	—	—	23.07	23.09
	2	25.52	24.36	29.55	29.75	24.70	24.99	27.15	27.99	25.24	26.21	29.51	29.50
	3	35.19	35.20	38.51	36.04	31.54	32.18	35.01	35.74	30.24	30.38	33.44	33.85
	4	39.59	40.17	41.16	42.14	33.88	34.98	39.32	40.58	38.77	38.44	40.37	41.48
	5	43.68	44.63	44.07	45.18	38.41	40.07	40.18	42.63	40.30	43.55	41.70	44.32
	6	45.16	46.81	45.01	47.05	42.10	43.05	41.36	43.82	43.26	45.15	43.37	45.91
	7	47.02	48.70	44.69	47.02	42.59	44.98	43.84	48.44	47.66	50.62	46.47	48.73
	8	47.50	51.01	47.27	51.65	44.67	48.02	47.37	48.37	48.04	53.04	46.97	50.16
	9	48.27	50.74	48.34	53.51	49.84	52.86	46.85	49.39	46.67	51.62	46.41	50.77
	10	53.16	55.25	47.74	52.05	50.86	54.21	46.04	52.73	46.03	57.03	48.00	49.52
	11	50.11	55.56	48.13	46.79	50.57	53.85	—	—	—	—	54.10	54.00
	12	—	—	—	57.00	—	54.00	—	—	—	—	55.07	—
Parameter sets for original data	L_∞	50.06	55.22	48.14	53.03	52.36	58.40	47.26	54.37	48.21	66.25	58.69	56.34
	K	−0.47	−0.37	−0.47	−0.42	−0.25	−0.21	−0.38	−0.28	−0.38	−0.18	−0.19	−0.24
	t_0	0.68	0.63	0.29	0.61	−0.30	0.42	0.10	−0.09	0.26	−0.61	−1.18	−0.75
	σ	1.63	1.58	0.94	2.94	2.52	1.45	1.32	1.31	1.87	1.70	2.30	1.40
Parameter sets for ages 0, 2-8	L_∞	51.649	57.855	48.948	54.288	47.651	52.515	49.848	51.970	52.271	59.788	48.496	53.118
	K	−0.328	−0.265	−0.396	−0.328	−0.323	−0.284	−0.319	−0.315	−0.302	−0.256	−0.383	−0.331
	t_0	−0.036	−0.052	−0.019	0.012	0.011	0.023	−0.004	−0.015	0.021	0.062	0.018	0.021
	σ	1.228	1.429	1.349	1.246	0.940	1.013	1.603	1.132	1.363	1.686	1.157	1.074
	Δ70 YC	+0.96	+1.25	+0.65	+0.66	−0.49	−0.53	+1.46	+0.91	−1.85	−2.47	−1.88	−2.02
	Δ67 YC	+0.24	−0.59	−1.69	−2.48	+0.34	+0.59	−2.23	−1.50	−0.86	−2.16	−0.95	−0.82

		Shelikof				Kenai	
		May-June 73		Aug.-Sept. 73		July-Aug. 75	
Item		M	F	M	F	M	F
		(0.17)		(0.42)		(0.33)	
Years of age (t)	1	—	—	20.71	20.74	21.92	21.23
	2	23.95	24.04	28.30	29.38	26.47	29.00
	3	30.37	30.64	32.71	33.52	31.84	32.58
	4	35.75	36.37	36.86	37.48	36.43	38.13
	5	38.86	40.34	38.71	39.20	37.94	39.65
	6	41.42	44.18	40.06	42.09	43.04	45.65
	7	49.01	46.50	45.32	47.51	[2]43.33	50.37
	8	49.41	49.29	43.94	46.52	51.06	51.32
	9	46.49	47.82	45.21	47.77	51.72	54.10
	10	47.00	49.85	45.60	48.39	53.00	—
	11	—	—	—	44.00	53.45	53.22
	12	—	—	—	—	—	55.44
Parameter sets for original data	L_∞	49.48	52.92	46.62	46.50	62.63	57.60
	K	−0.34	−0.28	−0.33	−0.39	−0.10	−0.22
	t_0	0.26	0.05	−0.31	−0.06	−1.50	−0.71
	σ	2.42	0.90	1.16	2.29	1.72	1.88
Parameter sets for ages 0, 2-8	L_∞	55.974	56.041	45.010	47.592	54.591	54.274
	K	−0.253	−0.255	−0.405	−0.386	−0.274	−0.312
	t_0	0.042	0.019	0.018	0.031	0.089	0.069
	σ	1.846	0.466	1.561	2.002	2.832	2.579
	Δ70 YC	−0.23	−0.31	−0.94	−1.21	−3.66	−4.11
	Δ67 YC	−2.68	−0.18	−1.57	−1.46	+2.18	+1.17

[1]Age, increment (ΔT) for sample date.
[2]Extreme frequencies eliminated in computing mean length at age 7.

es to see whether differences agree, in direction, with those generated by use of synthetic cohort growth curves. In this comparison, only early season samples were considered. Both year classes indicated lower mean lengths than other year classes sampled at like ages.

Growth completion rates (K) were 0.34 in males and 0.28 in females, from surveys indicating prominence of the 1967 or 1970 year classes (Figure 3). A similar averaging of length-at-age in all remaining data gave higher K-values (0.40 and 0.35, respectively), possibly reflecting lower relative year class strengths. We also ranked relative percent frequency at each age within range 2-8 yr, then fitting lengths of ages within ranks, thus replacing the original time-area classifications. Extreme K-values (males 0.25, 0.38; females 0.24, 0.40) were associated with extreme ranks; however, at intermediate ranks fluctuations were considerable. The K-ranges from this rearrangement of the data are similar to those shown in Table 2 for the original data configurations by survey (males,

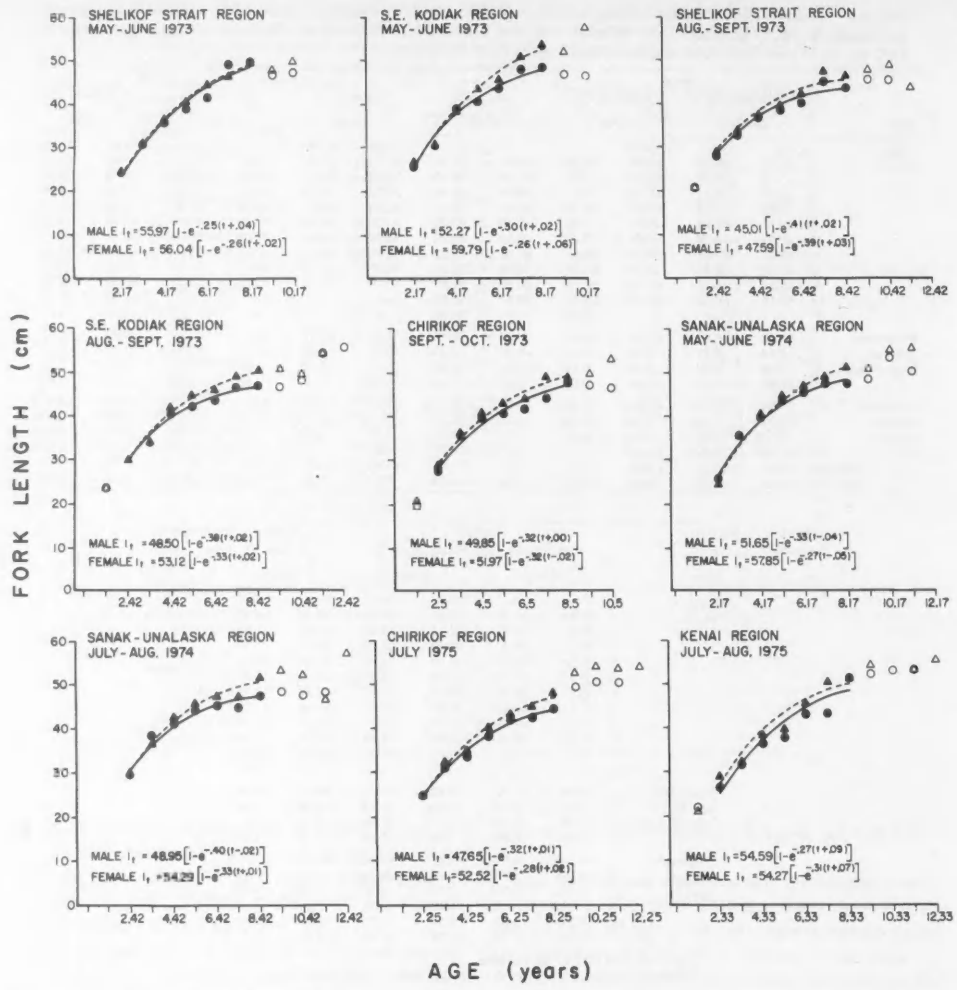
SHELIKOF STRAIT REGION
MAY - JUNE 1973
MALE l_t = 55.97 [1 - e^-.25(t+.04)]
FEMALE l_t = 56.04 [1 - e^-.26(t+.02)]
S.E. KODIAK REGION
MAY - JUNE 1973
MALE l_t = 52.27 [1 - e^-.30(t+.02)]
FEMALE l_t = 59.79 [1 - e^-.26(t+.06)]
SHELIKOF STRAIT REGION
AUG. - SEPT. 1973
MALE l_t = 45.01 [1 - e^-.41(t+.02)]
FEMALE l_t = 47.59 [1 - e^-.39(t+.03)]
S.E. KODIAK REGION
AUG. - SEPT. 1973
MALE l_t = 48.50 [1 - e^-.38(t+.02)]
FEMALE l_t = 53.12 [1 - e^-.33(t+.02)]
CHIRIKOF REGION
SEPT. - OCT. 1973
MALE l_t = 49.85 [1 - e^-.32(t+.00)]
FEMALE l_t = 51.97 [1 - e^-.32(t-.02)]
SANAK - UNALASKA REGION
MAY - JUNE 1974
MALE l_t = 51.65 [1 - e^-.33(t-.04)]
FEMALE l_t = 57.85 [1 - e^-.27(t-.05)]
SANAK - UNALASKA REGION
JULY - AUG. 1974
MALE l_t = 48.95 [1 - e^-.40(t-.02)]
FEMALE l_t = 54.29 [1 - e^-.33(t+.01)]
CHIRIKOF REGION
JULY 1975
MALE l_t = 47.65 [1 - e^-.32(t+.01)]
FEMALE l_t = 52.52 [1 - e^-.28(t+.02)]
KENAI REGION
JULY - AUG. 1975
MALE l_t = 54.59 [1 - e^-.27(t+.09)]
FEMALE l_t = 54.27 [1 - e^-.31(t+.07)]
FORK LENGTH (cm)
AGE (years)

FIGURE 6.—Growth curves of male and female walleye pollock by survey region and season in the western Gulf of Alaska, 1973-75.

0.25, 0.41; females, 0.26, 0.39). The arithmetic means of K in Table 2 (ages 2-8) are 0.33 and 0.30 and the geometric means of L_∞, 50.39 and 54.06 cm for males and females, respectively. Significant negative correlation between ln L_∞ and $|K|$ was found in both sexes. The highest observed ages in each survey lie, on the average, between those ages when growth is theoretically between 95 and 97.5% complete, according to the growth parameters for ages 2-8 in Table 2. Similarity in this regard is considered essential in estimating average natural mortality rates from empirical data (Alverson and Carney 1975).

Yield Relations

For management purposes natural mortality (M) as well as growth rate is needed for recogni-

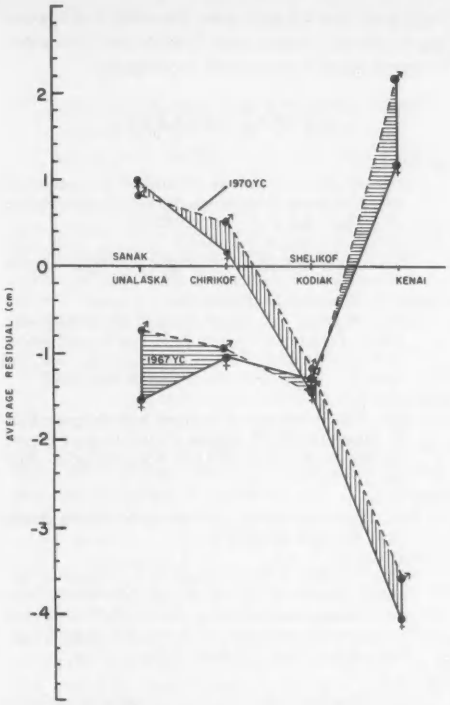

FIGURE 7.—Average of residuals from fit of observed mean length-at-age, taken over all age-groups of the 1967 and 1970 year classes of walleye pollock sampled in the western Gulf of Alaska by region and sex, 1973-75.

tion of optimality in biomass relations. Since no independent estimates of M are available for Gulf of Alaska pollock, we shall assume $M = K$. Yield relations based on this assumption have been examined in detail by Alverson and Carney (1975) for cases where the third Bertalanffy parameter (t_0) is close to zero. In the preceding section and Table 2, such growth estimates were provided.

As indicated earlier, means of observed female lengths at first maturity ranged from 30 to 35 cm, comparable to 32-37 cm when length at this stage is considered as two-thirds of the final length (L_∞) associated with the extreme growth completion rates for females in Table 2 (0.386, 0.255). Use of this constant was discussed and examined by Holt (1962). Corresponding ages at first maturity (T_{mat}) ranged from 2.84 to 4.30 yr, and ages of maximum (unfished) biomass per unit input (T_{mb}) ranged from 3.60 to 5.45 yr, according to equation 5 of Alverson and Carney (1975). The differences ($T_{mb} - T_{mat}$) at each extreme imply two annual pre-T_{mb} spawnings in the low-K cohort compared to one in the high-K cohort. The maximum production per unit input from the low-K (0.255, L_∞ = 56.04) cohort exceeds that for the high-K (0.386, L_∞ = 47.59) cohort by 64% assuming a cubic length-weight relation. Under the assumption $M = K$, any environmental or fishing conditions tending to reduce growth completion rate (and increase L_∞) would be expected to increase cohort productivity as well as delay the achievement of maximum biomass per unit input. Such a delay also implies an increased number of spawning opportunities for females prior to the age at maximum biomass.

DISCUSSION

Pollock size and age composition, size and age at first maturity, sex composition, length-weight relationship, density distribution by depth and area, estimate of exploitable biomass, in addition to growth and yield relationships in the western Gulf of Alaska have been described. The survey area, Cape Cleare to the western end of Unalaska Island, carries an exploitable pollock biomass that we have calculated at 0.6-1.2 million t. Compared with the 54,000 t of exploitable pollock in the central and eastern portions of the Gulf of Alaska (Ronholt et al.[3]), the resource described in this report represents over 90% of pollock in the Gulf of Alaska.

Agreeability of size, age, and growth data between surveys over the 3-yr study period indicated that assessment techniques were reliable. Weighting size and age composition data by catch rate and square miles within each depth sampling stratum is regarded as desirable when dealing with a species which displays bathymetric preference. Such weighting procedures coupled with the collection of otoliths over all depths and areas appear to provide accurate descriptive information for a large region. It is possible that pollock display bathymetric variations in growth rate as Westrheim (1973) has shown for Pacific ocean perch. However, our data did not allow such de-

[3]Ronholt, L. L., H. H. Shippen, and E. S. Brown. 1976. An assessment of demersal fish and invertebrate resources of the northeastern Gulf of Alaska, Yakutat Bay to Cape Cleare, May-August 1975: NEGOA Annual Report. Unpubl. manuscr., 184 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98112.

tailed examination, and the above sampling and analytical procedures would average this phenomenon if it does occur.

Data presented indicate that at least 87% of the pollock resource resides at depths 91-270 m during the summer with greater bathymetric dispersement during the spring. Densities were lowest in the Kenai region (eastern extreme) and highest in the Sanak-Unalaska region (western extreme). Except for the Kenai and Shelikof regions, where densities were notably low relative to other regions, regional biomass estimates are a function of both pollock density and available shelf or slope area at depths of 91-270 m.

Age and size composition data indicated that strong variations in year-class strength occur and recruitment of year classes is not uniform over the western Gulf. Whereas such geographic variations in year-class strength could be caused by environmental conditions, neither of two prominent year classes (1967 and 1970) indicated similar relative abundance over the entire east-west range of these surveys. Rather, the 1967 year class appeared in high density only west of southeast Kodiak and the 1970 year class, only at southeast Kodiak and eastward. These geographic density differences were accompanied by observed growth differences (size at age) and by negative departures of observed size at age in these year classes from expected size based on growth curve fits (Figure 7).

Analysis of all the growth information from these surveys indicated an inverse relation of growth completion rate (K) to relative year-class strength as well as to final estimated fish length (L_∞). From the differences in K values obtained and assuming $M = K$, it is inferred that optimally timed harvests per unit input would be larger in low-K cohorts than in high-K cohorts. Optimal timing from the yield standpoint also implies enhancement of the reproductive potential of low-K cohorts.

In conclusion, the western Gulf of Alaska pollock stock has been described and biological parameters reported for management. It is suggested that an east-west separation of spawning stocks may occur near Kodiak and that management should be applied accordingly.

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NOTES

ZOOPLANKTERS THAT EMERGE FROM THE LAGOON FLOOR AT NIGHT AT KURE AND MIDWAY ATOLLS, HAWAII

Many zooplankters in nearshore marine habitats are in the water column at night, but spend the daytime sheltered on or near the sea floor (Emery 1968; Glynn 1973; Porter 1974). The diel movements these organisms make between the water column and the sea floor are major features of nearshore ecosystems, and strongly influence many of the fishes in these habitats (Hobson 1968, 1973, 1974, 1975; Hobson and Chess 1976, 1978). Some of these zooplankters are holoplanktonic forms that swarm close to bottom structures by day and disperse above the reef at night. Included are various calanoid copepods (e.g., *Acartia* spp.), cyclopoid copepods (e.g., *Oithona* spp.), mysids (e.g., *Mysidium* spp.), and larval fishes (Emery 1968; Hobson and Chess 1978). Although such forms often occur in caves and other reef openings large enough to accommodate their free-swimming habit, they should be distinguished from the many meroplanktonic forms that by day live in or on the substrate (although this distinction between meroplankton and holoplankton is not always clear-cut).[1] At least some of these neritic holoplankters seem just loosely associated with specific substrata. For example, by day the calanoid *A. tonsa* swarmed close to coral reefs in the tropical Atlantic (Emery 1968) and to kelp forests in the warm temperate eastern Pacific (Hobson and Chess 1976), and also occurred in open waters offshore (Fleminger 1964). The meroplanktonic forms which by day characteristically assume what is essentially a benthonic mode have a much stronger affinity to specific nearshore substrata, and these are the major topic of this paper. Included are various polychaetes, ostracods, copepods, mysids, cumaceans, tanaids, isopods, gammarid amphipods, and various larval forms (Hobson and Chess 1976, 1978, in prep.).

Two recent studies, one on the Barrier Reef (Alldredge and King 1977) and the other in the Philippine Islands (Porter et al 1977; Porter and Porter 1977), have attempted to quantify the emergence of zooplankters from various coral-reef substrata. These are important papers because they draw attention to what unquestionably is a highly significant and long-neglected aspect of nearshore ecosystems. We suspect, however, that there are problems with these studies. If so, the problems should be promptly recognized because undoubtedly they will spawn similar investigations by other workers elsewhere (e.g., see Randall et al. 1978). Alldredge and King collected their samples in Plexiglas[2] traps that rested on the bottom and retained organisms that rose into the water column; however, zooplankters from the surrounding water had access to these traps through gaps between the traps' rigid lower edges and irregularities on the sea floor. Earlier (Hobson and Chess 1978), we stated that these collections need to be repeated with this possibility of error eliminated. Obviously, if many zooplankters entered the traps from the surrounding water column, the samples cannot be considered measures of the organisms that emerged from the underlying substrata. The Porter group used traps that were tethered above the sea floor, and so would seem to have offered even greater access to zooplankters from the surrounding water. In fact, the probability that such forms entered the traps seems to us so great that we would have expected that their intent was simply to sample zooplankters near the reef. And yet, in prefacing their findings with statements like (p. 107) ". . . volumes of plankton produced per m^2 per hour by different reef substrates during the day and during the night are given in Table 1." they clearly implied that each trap sampled only those organisms that had risen from the substrate directly below it.

Our doubts about these studies, however, were moderated by limitations in our own knowledge of the phenomenon. We had worked extensively with these activity patterns as they relate to fishes (Hobson 1968, 1974; Hobson and Chess 1976, 1978) and had made inferences about the daytime modes of nocturnal zooplankters in nearshore habitats. Still, we had not satisfactorily distin-

[1] We define meroplankton as those zooplankters that are in or on the substrate during part of the diel cycle, and holoplankton as those that are in the water column at all hours. As pointed out earlier (Hobson and Chess 1976), these terms have carried different meanings for different authors.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

guished the forms that by day assume essentially a benthonic existence on or in the bottom, from the forms that by day aggregate close to, yet free of, the substrate, or which migrate to deeper water. To increase our understanding of these activities and to acquire a firmer base upon which to assess other studies, we trapped zooplankters that emerged from various substrata in the lagoons of Kure and Midway Atolls, Hawaii during August 1977, making special effort to exclude forms from the surrounding water column.

Methods

Midway and Kure Atolls are about 90 km apart at the northwestern end of the Hawaiian Archipelago. They are very similar, each having a lagoon that is relatively small (diameter about 8 km) and shallow (maximum depth about 15 m). All our study sites were in approximately 5 to 7 m of water near the outer leeward reefs.

We made seven paired collections, each pair at a different location. One of each pair sampled the organisms that rose from the substrate during the day, and the other sampled the organisms that rose from the same spot during the night. Of the substrates sampled, three were sand (two at Midway, one at Kure), two were a mixture of sand and coral rubble (one at Midway, one at Kure), and two were small heads of both living and dead coral

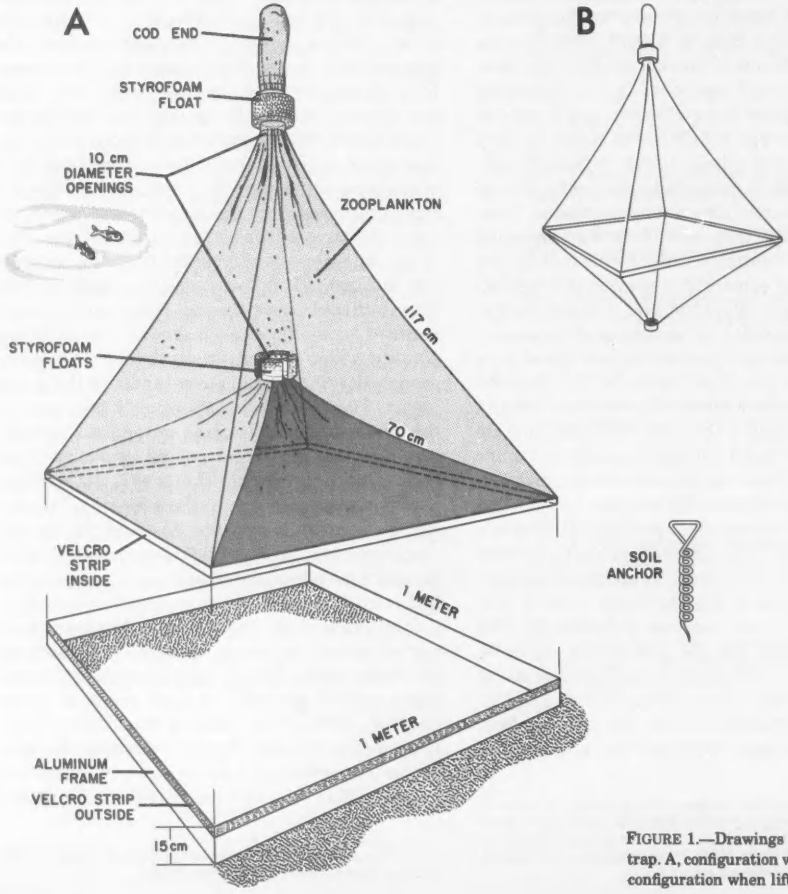

FIGURE 1.—Drawings of the meroplankton trap. A, configuration when set on bottom; B, configuration when lifted by diver.

(about 0.25 to 0.40 m²) surrounded by sand and coral rubble (one at Midway, one at Kure).

It was not our intent to characterize the meroplankton from each substrate—the collections were too few for this; rather, we sought only a general understanding of the types and numbers of organisms that emerge from the lagoon floor.

To begin each set of collections, we placed our trap (Figures 1, 2) in position between sunrise and 0800 h. First we buried the lower portion of the metal frame in the sand and secured it with soil anchors. A tight seal around the base of the trap was judged critical to prevent entry by organisms from the surrounding water. Next we attached the net (which had a 0.333-mm mesh) to this base and allowed it to remain in position throughout the day. We retrieved the net between 1730 h and sunset, washed all materials into the cod end, then removed the materials, and placed them in 10% Formalin. The net, with an empty cod end in place, was then reattached to the frame and left in place throughout the night. The following morning, again between sunrise and 0800, the entire trap—base as well as net—was retrieved, and the collected organisms placed in preservative as before. Having thus completed one set of collections, we moved to another site and repeated the procedure. (We would have reversed the order of collections in some sets, e.g., nighttime first, if appreciable numbers of organisms had been taken by day; as it turned out, however, essentially all organisms were taken in the nighttime samples, as detailed in the Results.)

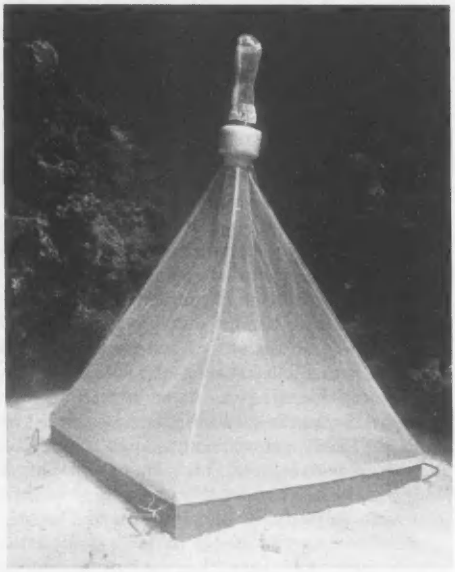

FIGURE 2.—The meroplankton trap in place to sample organisms that emerge from sand in the lagoon of Midway Atoll. If the trap had not been designed to exclude holoplankters, we believe the collections would have included, among other holoplankters, calanoid copepods (*Acartia* sp.) that swarmed close to the adjacent reefs by day, including at their bases, and dispersed throughout the area at night.

Our trap worked as follows: Organisms rising from the substrate inside the trap swam upward through the small upper opening of the inner cone and entered the space within the larger outer cone (Figure 1A). Some may have continued up into the cod end, which floated above, but this had no bearing on the collections. When the organisms returned toward the sea floor all except those that happened to descend through the small orifice of the inner cone were trapped where the two cones converged at their common base. In retrieving the net, we reached in under the edge attached to the metal frame and grasped the inner cone around its smaller orifice, thus closing it. We then pulled this out, thus everting the inner cone and producing a diamond-shaped bag (Figure 1B) with the orifice closed in our grasp at one end and the cod end at the other. We then towed the net back to the boat, still enclosing the smaller orifice in our grasp, so that, as we swam, all materials inside were swept back into the trailing cod end.

Results

The organisms collected by our trap, day and night, are listed in Table 1. The general absence of organisms in the daytime collections was predictable, based on the many reports which have concluded that the diel emergence of such forms is primarily a nocturnal phenomenon (see references listed above). Among organisms we observed swarming close to reef structures in the vicinity of our trap during the day were calanoid copepods (most of them *Acartia* sp.), mysids, and larval fishes. Although such forms disperse in the water column at night (Emery 1968; Hobson and Chess 1976, 1978), their absence from our trap collections is consistent with the contention that the holoplanktonic forms associated in varying degree with the reef are distinct from those organisms that live by day in or on the substrate.

TABLE 1.—Organisms trapped by day and night at Kure and Midway Atolls.

Zooplankton category	Day (n = 7)		Night (n = 7)	
	Percent occurrence	Mean no. individuals	Percent occurrence	Mean no. individuals
Foraminiferans[1]	43	2.9	100	18.9
Polychaetes[2]	29	0.5	100	7.3
Gastropods[3]	57	0.1	100	7.0
Ostracods[4]	0	0.0	86	1.7
Calanoid copepods[5]	0	0.0	100	17.7
Cyclopoid copepods	0	0.0	43	1.4
Harpacticoid copepods[6]	0	0.0	100	31.0
Mysids	0	0.0	14	0.1
Cumaceans	0	0.0	29	0.6
Tanaids[7]	0	0.0	86	11.9
Isopods[8]	0	0.0	71	3.0
Cirripedian larvae	0	0.0	29	0.6
Gammarid amphipods[9]	0	0.0	100	40.1
Caprellid amphipods	0	0.0	43	1.0
Caridean larvae	0	0.0	43	60.9
Caridean adults and juveniles	0	0.0	86	18.4
Reptantian zoea	0	0.0	57	17.0
Brachyuran megalops	0	0.0	71	6.3
Anomuran glaucothoe	0	0.0	43	1.3
Chaetognaths[10]	0	0.0	57	5.9
Ascidian larvae	0	0.0	14	1.0

[1]All foraminiferans were either *Tretomphalus* sp. (72%) or *Amphistigina* sp. (28%).
[2]The major polychaete was *Polyophthalmus* sp.
[3]Included one 8-mm dorid opisthobranch; the rest were prosobranchs <3 mm long.
[4]The major ostracod was a species of Cylindroleberdinae.
[5]All identifiable calanoids were *Paramisophria* sp., probably undescribed (Abraham Fleminger, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978).
[6]All identified harpacticoids were of a species of the family Peltidiidae.
[7]All the tanaids appeared to be of a species of *Leptochelia*, close to *L. dubia* (see Hobson and Chess 1976).
[8]Major isopods were: *Ciroiana* sp., *Ianiropsis* sp., *Munna* sp., anthurids, and cryptoniscid larvae.
[9]Gammarids included: *Aoroides* sp., *Dexaminoides orientalis*, *Lilgeborgia* sp., a eusirid, an oedicerotid, and a phoxocephalid.
[10]All chaetognaths were *Spadella gaetanoi* (A. Alvarino, Fishery Biologist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. commun. Sept. 1978).

Discussion

Our collections and collecting sites were too few to comprehensively quantify the zooplankters that emerge from the lagoon substrata at Kure and Midway Atolls. Despite its limitations, however, this study increases our understanding of the kinds of organisms that have this habit. Furthermore, it indicates there may be serious problems with the more extensive studies of Alldredge and King (1977), Porter et al. (1977), and Porter and Porter (1977).

Certainly some of the differences between their samples and ours are unrelated to sampling problems. We assume, e.g., that the zooplankton fauna at Kure and Midway Atolls is distinguishable from the zooplankton fauna in the more tropical latitudes of the western Pacific Ocean where the Alldredge and Porter groups studied. It is unlikely, however, that zoogeographic variations can account for certain of the more striking differences between their samples and ours. The predominant forms in their collections were calanoid and cyclopoid copepods. Alldredge and King (1977) calculated that during the night a mean of 6,679 calanoids emerged from each square meter of the reef face, and Porter et al. (1977) reported that over 10,000 calanoids emerged during the night from each square meter of branching coral in their study area. In comparison, our night-long collections from a variety of substrata, including coral, yielded a mean of only 17.7 calanoids/m^2. Of course, we did not sample a well-developed reef. Only two of our sites included living coral, and these were isolated heads (our traps required a bed of sand). So habitat features could have contributed differences between the collections. Nevertheless, if one considers the species of calanoids and cyclopoids collected by Alldredge and King, there are strong indications that the large numbers reported were inflated by holoplanktonic forms. The only calanoids and cyclopoids they identified were *Acartia* spp. and *Oncaea* spp. Species of these two genera are exceedingly numerous in the water column during both day and night (see Emery 1968; Hobson and Chess 1976), and we question whether they could in fact assume a benthonic mode. As stated (Hobson and Chess 1978:149) "We would expect organisms that live in the substrate by day to have morphological features reflecting this habit that distinguish them from holoplanktonic relatives at the generic level or higher." Although the Porter group did not identify their calanoids and cyclopoids to lower taxa, they too sampled western Pacific reefs and so the copepods that similarly dominated their collections may well have been the same, or very similar, to those taken by Alldredge and King. All our calanoids, on the other hand, appeared to be referable to the little known genus *Paramisophria* (Abraham Fleminger, Associate Research Biologist, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978). This fact agrees with our contention that zooplankters which periodically enter the substrate should be morphologically distinctive. If the diurnal benthic mode of this species is a generic characteristic, which seems probable, then its poorly known status likely stems from failure to be sampled by standard plankton-collecting techniques.

During a marine survey of the Palau Islands, Randall et al. (1978) attempted to measure the zooplankters that emerged from the sea floor using traps ". . . built according to the design of Porter

and Porter (1977)." Their samples, taken above coral and sand substrata, included far fewer copepods than the Alldredge and Porter collections (but many more than ours); nevertheless, they recognized the presence of holoplanktonic forms (e.g., siphonophores, crustacean and fish eggs, and fish larvae), which they assumed ". . . either swam (or were carried) under the base of the trap from the open water . . .."

So we believe that the studies by the Alldredge and Porter groups are flawed by the unrecognized occurrence in their samples of organisms from the surrounding water column. At Enewetak Atoll (Hobson and Chess 1978), we concluded that many of the zooplankters above lagoon reefs at night are visitors from the deeper water. If this circumstance existed where Alldredge and Porter set their traps, then their collections probably included deep-water forms. If so, the figures presented as measures of zooplankters that emerge from defined areas of particular nearshore substrata probably include not only holoplankters associated by day with other nearshore substrata but also holoplankters from outside the nearshore realm.

We consider our collectons conservative estimates of the numbers of organisms that emerge from the sampled substrata. It may be that some forms which ordinarily rise into the water column were inhibited by our trap, and undoubtedly some that rose into the trap found their way back to the sea floor. But we feel our trap should have been as effective in capturing emerging zooplankters as those used by the Alldredge and Porter groups. Possibly some strictly benthic forms entered our samples by climbing up the inside of the trap. The few prosobranch gastropods that were taken may have been trapped this way, although they were small enough to have been swept up into the water column by surge, or perhaps to possess some flotation device that periodically permits a planktonic mode, as is the case with certain foraminiferans (e.g., *Tretomphalus* and perhaps *Amphistigina*). Significantly, most of the organisms collected belong to groups that include forms we have collected in the water column at night elsewhere: e.g., the foraminiferan genus *Tretomphalus* (at Majuro and Enewetak Atolls: Hobson and Chess 1973, 1976); the polychaete genus *Polyophthalmus* (at Enewetak Atoll: Hobson and Chess 1978); and the ostracod subfamily Cylindroleberdinae, the tanaid genus *Leptochelia,* the isopod genera *Cirolana* and *Munna*, and family Anthuridae, the gammarid genus *Aoroides,* and families Eusiridae, Oedicerotidae, and Phoxocephalidae (at Santa Catalina, southern California: Hobson and Chess 1976, in prep). The forms that predominated in our collections belong to groups that were only relatively minor elements in the Alldredge and Porter collections. Most, in fact, were lumped by Porter et al. (1977) in their summarizing Figure 2 as "miscellaneous." This is not because they took fewer of these forms than we did, but rather because copepods and larvaceans so dominated their collections.

We believe that the major difference between our collections and those of the Alldredge and Porter groups is that we excluded organisms from the surrounding water column. Alldredge and King (1977) were aware that outside organisms could enter through the gaps around the base of their traps, but seemed more concerned about organisms inside that might have escaped. They dismissed both possibilities as significant sources of error with the statement (p. 318) ". . . as many plankters may also enter the trap through these gaps as escape through them." But because these devices were, after all, traps, probably many more zooplankters came in than went out. And if in fact zooplankters entered the traps through these gaps, it seems certain that forms from the surrounding water, including holoplankters, were continuously captured. Porter et al. (1977) reported about 1.5 to 2 times as many zooplankters as did Alldredge and King. They attributed this difference to more effective methods and equipment, but their traps, tethered above the reef, may simply have been more readily entered by holoplankters. This would also account for the relatively large numbers of zooplankters they trapped by day. Both studies may have suffered from a misconception about the movements of these organisms. Alldredge and King doubted that many escaped through the gaps around the bases of their traps because they assumed (p. 318) ". . . emerging plankton swim primarily upward . . . ." The Porter group would seem to have based their trap design —inverted cones tethered above the bottom—on the same assumption. But while these animals certainly rise progressively higher in the water column after emerging from the sea floor, generally they swim—some flit—in short, irregular tangents more horizontal than vertical (based on our direct observations of a wide variety of forms in many locations). In any event if holoplankton did enter these traps in significant numbers, then

the samples taken should not be presented as measurements of the forms that emerged from the underlying substrata.

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A SURVEY OF HEAVY METALS IN THE SURF CLAM, *SPISULA SOLIDISSIMA*, AND THE OCEAN QUAHOG, *ARCTICA ISLANDICA*, OF THE MID-ATLANTIC COAST OF THE UNITED STATES

Since the mid-1940's, two varieties of clams have become increasingly important to the seafood industry, the surf clam, *Spisula solidissima* , and the ocean quahog, *Arctica islandica*. Surf clams and ocean quahogs are marketed primarily by the canning industry in chowders or as minced clams, as well as in a number of specialty products, such as cakes, patties, and dips. Prior to World War II, however, these clams had been used only as animal feed or fertilizer. A commercial surf clam fishery developed rapidly with an annual harvest of 51.4 million pounds of meats in 1977 (Hutchison[1]) and a peak harvest of 96.1 million pounds of meats in 1974 (Bell and Fitz Gibbon 1977). The ocean quahog fishery developed more slowly. It was not until the 1970's that a vigorous commercial ocean quahog fishery developed, primarily to supplement the dwindling supplies of more desirable clams, in particular, the hard clam, *Mercenaria mercenaria*; the soft-shell clam, *Mya arenaria*; and the surf clam (Anonymous 1971). The ocean quahog harvest in 1977 of 16.4 million

[1]Roger Hutchison, U.S. Department of Commerce, Economic and Marketing Research Division. Washington, D.C., pers. commun. February 1978.

pounds of meats (Hutchison see footnote 1), however, represents a small fraction of an estimated sustained yield of 86 million pounds of meats annually (Rinaldo[2]).

Since surf clams and ocean quahogs have replaced many traditional species, studies are needed that reflect their economic importance. It is well documented that many molluscs, including surf clams and ocean quahogs, concentrate heavy metals (Brooks and Rumsby 1965; Pringle et al. 1968; Waldichuk 1974). Boyden (1973) stated that one of the nutritious qualities of shellfish may be their high metal content. However, heavy metals exhibit toxic effects that affect all life stages of shellfish, especially development stages (Calabrese et al. 1973; Calabrese and Nelson 1974; Thurberg et al. 1975). Considerable research has been done on effects of heavy metals on more popular species of bivalve molluscs, especially the American oyster, *Crassostrea virginica*, hard clams, and soft-shell clams (Calabrese et al. 1973; Calabrese and Nelson 1974; Thurberg et al. 1974). However, until recently, there has been little interest in surf clams or ocean quahogs. Concentrations and concentration factors for a number of metals, including cadmium, chromium, copper, lead, nickel, and zinc, have been given by Pringle et al. (1968) and Pringle and Shuster[3] for surf clams taken from Atlantic coast waters (Maine through North Carolina). Thurberg et al. (1975) exposed larval, juvenile, and adult surf clams to sublethal doses of silver and measured both physiological responses and bioaccumulation. Researchers at the U.S. Environmental Protection Agency (EPA), Narragansett, R.I., have exposed ocean quahogs to low concentrations of cadmium and monitored toxicological, biological, and histopathological effects, as well as bioaccumulation (Zaroogian[4]). Bioaccumulation distribution patterns associated with industrial and sewage sludge dumpsites southeast of Delaware Bay have been monitored in ocean quahogs by scientists at the EPA, Annapolis, Md. (Lear and Pesch 1975). Awareness, then, of the importance of these species is developing, but clearly more research is needed for such an important commercial shellfishery.

Nine metals were chosen for analysis: arsenic, cadmium, chromium, copper, lead, mercury, nickel, silver, and zinc. Based upon estimates of global metal production and oceanic sedimentation rates, Bowen (1966) divided 38 metals into their pollution potentials. He categorized cadmium, chromium, copper, lead, mercury, silver, and zinc as very high potential pollutants and arsenic and nickel as moderate. Goldberg (1972) emphasized the need for measurement in benthic organisms of the most potentially hazardous trace metals.

Materials and Methods

Sampling

The area of this survey extended from approximately Montauk Point, N.Y., to Cape Hatteras, N.C., and seaward to approximately the 20-fathom contour. The survey encompassed the southern distribution of both surf clams and ocean quahogs in the United States. Samples were collected at 151 stations for chemical analysis (Figure 1) in June and August 1974, aboard the NOAA ship *Delaware II* (MARMAP[5]). A small hydraulic surf clam dredge, modeled closely after larger commercial dredges, was used throughout the survey. At each station 4-6 clams of marketable size were dissected, using stainless steel equipment. The foot was removed from each animal, drained, then combined and frozen in plastic bags. At the laboratory the tissues were homogenized in an electric blender equipped with a glass jar and stainless steel blades then stored for analysis in plastic ointment jars. All containers and equipment were acid-washed prior to use.

Analysis

Mercury analysis was performed on a Perkin-Elmer Model 305[6] atomic absorption spectrophotometer fitted with a 25 × 150 mm absorption cell with silica end windows, using the flameless method of Greig et al. (1975).

Arsenic analysis, performed on a Perkin-Elmer Model 403 atomic absorption spectrophotometer,

[2]Rinaldo, R. G. 1977. Atlantic clam fishery management plan. Environmental impact statement: Mid-Atlantic and New England Regional Fisheries Management Councils. Available Fisheries Management Division, National Marine Fisheries Service, NOAA, State Fisheries Pier, Gloucester, MA 01930.

[3]Pringle, B. H., and C. N. Shuster, Jr. 1967. A guide to trace metal levels in shellfish. USDHEW, Public Health Serv., Shellfish Sanit. Tech. Rep., 18 p.

[4]Gerald E. Zaroogian, U.S. Environmental Protection Agency, Environmental Research Laboratory, Narragansett, RI 02882, pers. commun. February 1976.

[5]MARMAP 1974. Surf clam survey, cruise report, NOAA ship *Delaware II*, 13-28 June 1974 and 5-10 August 1974, 9 p.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

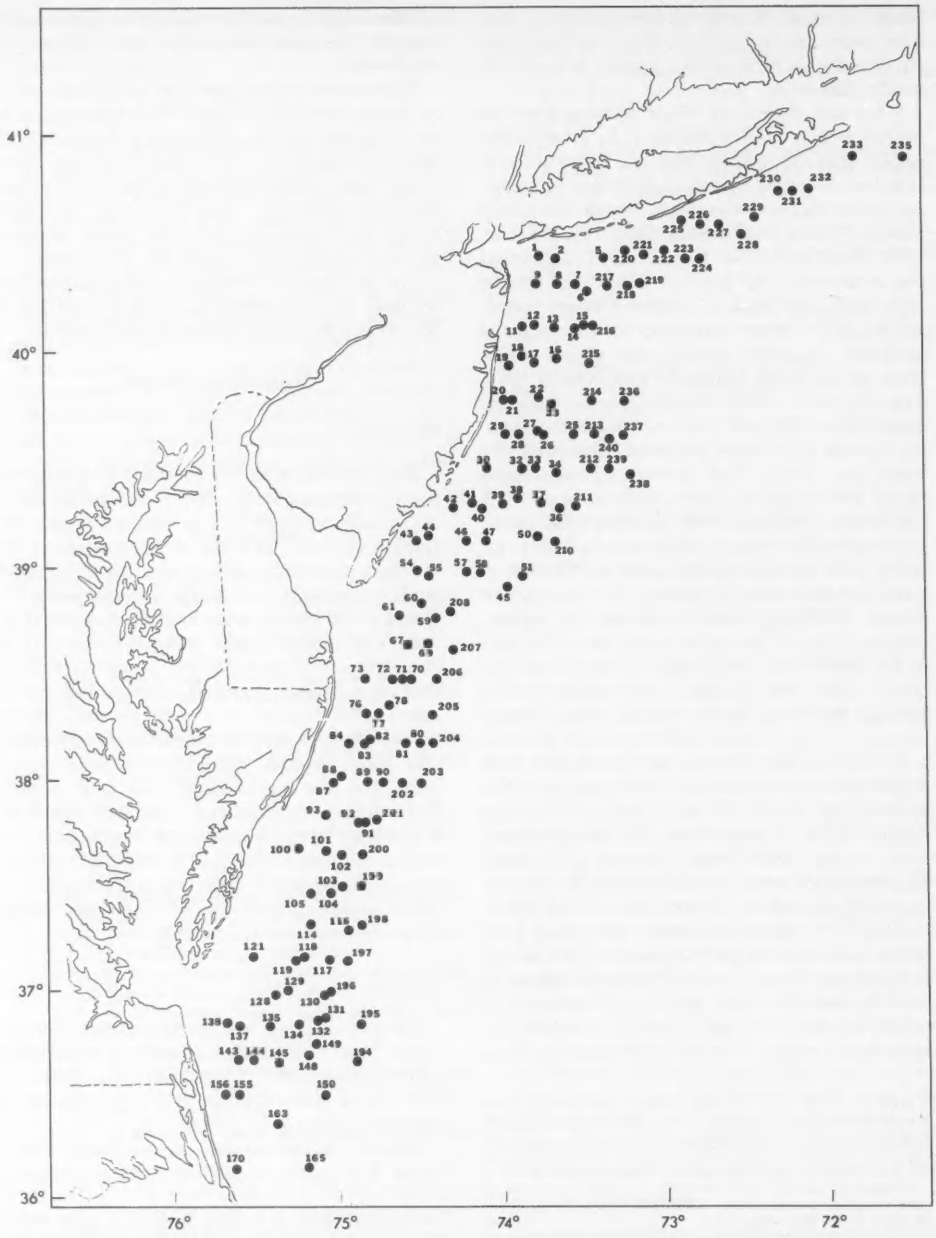

FIGURE 1.—Station location and number relative to the mid-Atlantic coast of the United States.

using a nitrogen/hydrogen flame, required an improvisation of two simple interconnecting adapters. The first, attached directly to the instrument, consisted of the female portion of a polyethylene quick disconnect (Nalgene 6150) and a nylon elbow hose connector threaded to fit the auxiliary inlet of the burner assembly. The second consisted of the male portion of the quick disconnect and a gas outlet adapter (Kontes K-183000). Both adapters were assembled with minimum length and bore of Nalgene tubing. The following procedure was used: A 5-g sample of tissue was placed into a 250-ml beaker to which 10 ml $Mg(NO_3)_2 \cdot 6H_2O$ (200 g/l) and 10 ml concentrated HNO_3 (Baker 9603) were added. The mixture was covered with a watchglass and evaporated to dryness on a hot plate (130°-140°C). It was then placed into a cool muffile furnace and the temperature raised in steps, first to 250°C for 3 h, then to 400°C for 3 h, and finally to 550°C for approximately 15 h. After the beaker was completely cool, 15 ml of concentrated HCL (reagent grade) were added and the resulting solution transferred to a 25-ml volumetric container and brought to volume with distilled water. A 10-ml aliquot of this solution was placed into a 24/40 jointed, 50-ml Erlenmeyer reaction flask and 2 ml of 15% (wt/vol) freshly made KI solution and 2 ml of freshly made $StCl_2$ solution (20% [wt/vol] in 1:1 concentrated HCL:water) were added, waiting 2 min after each addition. Then 10 ml of distilled water were added. Five (5.00) grams of granular (20 mesh, no fines) low arsenic zinc (Fisher Z-15) were placed into the elbow of the second adapter, as noted above, and attached to the first adapter. This assembly was quickly inverted while attaching it to the reaction flask. The arsine generated was then analyzed at the instrument, which was equipped with a 3-slot burner and background corrector. Use of a recorder combined with full noise filtration and slow gas evolution contributed to a smooth and reproducible peak upon which calculations were based. The reaction flask and the first adapter can be quickly removed for cleaning and reuse.

Analysis of the remaining metals, also performed on the Perkin-Elmer Model 403, resembled that of Middleton and Stuckey (1954): A sample of tissue (10 g wet weight) was weighed into a 250-ml beaker and 10 ml of concentrated HNO_3 (Baker 9603) were added. The beaker was covered with a watchglass and heated to approximately 130°-140°C on a hot plate until the liquid evaporated. One to two milliliters of concentrated HNO_3 was added and the evaporation repeated. Again, 1-2 ml of acid was added but evaporated at 350°C or more. The hot plate was cooled and the latter acid addition and evaporation was repeated until ashing was complete. The residue was dissolved in and taken up to 25 ml with 10% (wt/vol) reagent grade HNO_3 after filtration through Whatman No. 2 paper. The solution was then analyzed directly in an air/acetylene flame by conventional atomic absorption spectrophotometry.

Results

Greater average concentrations of silver, arsenic, cadmium, copper, and zinc (122, 44.5, >230, 56.0, and 10.9% greater, respectively) were found in ocean quahogs than in surf clams for the entire survey (Table 1). Concentrations of several metals in both clams decreased southward. Concentrations of silver decreased steadily from 2.62 to 0.58 ppm in ocean quahogs and 1.63 to 0.19 ppm in surf clams. This is a 4.5- and 8.6-fold decrease, respectively, from the northernmost range of latitude to the southernmost. Concentrations of arsenic also decreased steadily, 1.6-fold, from 3.90 to 2.41 ppm in ocean quahogs. Although a steady decrease in arsenic concentrations was noted for a full 2.5° of latitude, a distinctive trend for the entire range of latitude was not evidenced. Copper concentrations in ocean quahogs decreased 2.5-fold from 7.16 to 2.84 ppm and zinc concentrations in surf clams decreased 2.0-fold from 18.5 to 9.1 ppm. Concentrations of cadmium and zinc in the ocean quahog and copper in the surf clam did not exhibit any statistically significant trends, while the data for the remaining metal-clam combinations were insufficient for statistical analysis (Table 2).

The results of Pringle and Shuster (see footnote 3) for cadmium and zinc (<0.20, 12.39 ppm, wet weight, respectively) in surf clams are in general agreement with the mean results of our study. Their result for copper (2.39 ppm) was lower, while chromium and nickel (2.57, 1.22 ppm, respectively) were higher. The collection area of the former study was defined only as Maine through North Carolina; hence, geographic variations might be expected. In addition, neither the number of stations nor of surf clams analyzed was stated.

Conclusions

While the Food and Drug Administration (FDA)

TABLE 1.—Average[1] heavy metal concentrations (parts per million, wet weight) found in surf clams and ocean quahogs by latitude.

Range of lat. N	*n*	Ag		As		Cd		Cu		Zn	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Surf clams											
41°00′-40°30′	3	1.63	1.11	2.38	0.146	<0.12		3.83	0.786	9.7	0.674
40°30′-40°00′	6	1.42	.329	2.63	.234	0.13	0.008	2.87	.216	18.5	.481
40°00′-39°30′	11	1.18	.140	2.39	.120	0.13	.010	2.96	.348	18.3	1.14
39°30′-39°00′	11	1.05	.130	2.17	.200	0.15	.015	3.45	.226	14.8	1.11
39°00′-38°00′	13	0.94	.120	1.91	.131	<0.13		3.38	.211	11.3	.485
38°30′-38°00′	13	0.50	.082	1.57	.082	<0.11		2.97	.259	10.6	.188
38°00′-37°30′	8	0.51	.081	2.08	.145	<0.12		3.54	.360	9.1	.253
37°30′-37°00′	11	0.44	.071	2.22	.122	<0.12		3.48	.478	9.4	.228
37°00′-36°30′	14	0.32	.046	2.17	.233	<0.14		3.08	.228	9.3	.260
36°30′-36°00′	3	0.19	.053	1.46	.082	<0.14		2.88	.262	9.6	.153
41°00′-36°00′	93	0.76		2.08		<0.13		3.23		11.9	
Ocean quahogs											
41°00′-40°30′	8	2.62	0.400	3.90	0.374	0.54	0.069	7.16	0.837	12.6	0.518
40°30′-40°00′	15	2.49	.376	3.36	.293	0.42	.034	5.33	.401	14.5	1.04
40°00′-39°30′	9	1.53	.296	2.97	.171	0.42	.035	4.71	.348	13.9	.741
39°30′-39°00′	9	1.29	.138	2.68	.236	0.39	.035	4.41	.280	12.4	.991
39°00′-38°30′	5	1.21	.371	2.65	.114	0.42	.059	5.10	.727	13.2	.806
38°30′-36°30′	6	0.58	.120	2.41	.326	0.39	.051	2.84	.434	10.4	1.38
41°00′-36°30′	52	1.69		3.01		0.43		5.04		13.2	

[1]Average of *n* samples with 4-6 clams per sample.

TABLE 2.—Average[1] heavy metal concentrations (parts per million, wet weight) found in surf clams and ocean quahogs by latitude.

Range of lat. N	*n*	Cr	Hg	Ni	Pb
Surf clams					
41°00′-40°30′	3	<0.62	<0.05	—	<0.7
40°30′-40°00′	6	0.95	<0.07	0.71	<0.7
40°00′-39°30′	11	0.70	<0.08	<0.39	<0.7
39°30′-39°00′	11	0.69	<0.08	0.80	<0.7
39°00′-38°30′	13	0.65	<0.08	<0.60	<0.7
38°30′-38°00′	13	<0.61	<0.08	<0.50	<0.6
38°00′-37°30′	8	<0.53	<0.08	—	<0.7
37°30′-37°00′	11	<0.49	<0.07	—	<0.7
37°00′-36°30′	14	<0.48	<0.06	—	<0.7
36°30′-36°00′	3	<0.48	<0.05	—	<0.7
41°00′-36°00′	93	<0.61	<0.07	<0.59	<0.7
Ocean quahogs					
41°00′-40°30′	8	1.03	<0.09	0.91	1.8
40°30′-40°00′	15	<1.23	<0.06	<0.62	1.0
40°00′-39°30′	9	<0.70	<0.06	<0.50	<1.2
39°30′-39°00′	9	<0.80	<0.07	<0.50	<0.9
39°00′-38°30′	5	<1.0	<0.08	<0.55	<1.2
38°30′-36°30′	6	<1.1	<0.06	<0.59	<0.9
40°00′-36°30′	52	<1.0	<0.06	<0.61	<1.1

[1]Average of *n* samples with 4-6 clams per sample.

has not set standards for heavy metals in U.S. fishery products (except mercury), the National Health and Medical Research Council (NHMRC) of Australia has recommended maximum concentrations for a number of metals in seafoods (Mackay et al. 1975). Concentrations of cadmium, copper, lead, and zinc found in surf clams and ocean quahogs were well under these limits (2.0, 30, 2.0, 1,000 ppm, wet weight, respectively) and far below levels found in American oysters harvested from Atlantic coastal waters (Pringle et al. 1968). The NHMRC recommendation of 1.14 ppm (wet weight) arsenic (1.5 ppm as As_2O_3), however, was exceeded at all but a few sampling stations.

Mean arsenic concentrations for all stations were 2.1 ppm in surf clams and 3.0 ppm in ocean quahogs. The distribution of arsenic concentrations did not vary greatly with latitude and may indicate that background levels along the mid-Atlantic coast are higher than those in Australian waters. Concentrations of mercury were found to be well below the action limit set by the FDA (0.50 ppm, wet weight).

Major fishing grounds for the surf clam industry are located off the New Jersey and Virginia coasts. Since data for mercury presented in this study are well within the existing guideline set by the FDA for U.S. fishery products and, with a single exception, within the more extensive NHMRC recommendations for Australia, there should be little concern to consumers for surf clams or ocean quahogs harvested from these areas at present.

The latitudinal cline demonstrated in this study should, however, stimulate further interest in heavy metal inputs along the mid-Atlantic coast of the United States. Data indicate that a large area of our eastern coast may be affected by the presence of heavy metals. The effect on clams is important, particularly since surf clams and ocean quahogs are representative of the important shellfisheries located in this area.

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APPARENT FEEDING BY THE FIN WHALE, *BALAENOPTERA PHYSALUS*, AND HUMPBACK WHALE, *MEGAPTERA NOVAENGLIAE*, ON THE AMERICAN SAND LANCE, *AMMODYTES AMERICANUS*, IN THE NORTHWEST ATLANTIC

On 18 May 1977 a large group of fin, *Balaenoptera physalus*, and humpback, *Megaptera novaengliae*, whales was observed on Stellwagen Bank north of Cape Cod (lat. 42°26′N, long. 70°26′W) by Northeast Fisheries Center (NEFC) personnel conducting an annual spring bottom-trawl survey aboard the National Oceanic and Atmospheric Administration RV *Albatross IV*. Nine fin and 14 humpback whales were identified and observed near the vessel. More whales were sighted in the vicinity, but were too far away to identify positively or to observe conveniently. Many great black-back, *Larus marinus*, and herring, *Larus argentatus*, gulls were seen feeding at the surface and circling around the whales. The whales displayed a characteristic feeding behavior described by Gunther (1949) and mentioned in Katona et al. (1975). The animals we observed were circling, spouting often, making short shallow dives, and not moving in any set direction. They behaved in a leisurely manner and were seemingly undisturbed by our presence as noted by Gunther (1949). Echo sounding traces indicated a depth of 40 m in this area and large patches of densely concentrated small fishes throughout the water column, but particularly near the surface. During several 30-min bottom-trawl tows in the area, up to 400 kg of adult American sand lance, *Ammo-*

dytes americanus, were netted per tow (Northeast Fisheries Center[1]) with Atlantic cod, *Gadus morhua*, and spiny dogfish, *Squalus acanthias*, the only other abundant fish species. An examination of several cod stomachs showed them to be packed with sand lance while a similar inspection of sand lance showed them to be feeding on copepods. It is our contention that the abundance and behavior of whales in this area indicates that they were feeding on a concentration of American sand lance.

Similar whale feeding behavior had been previously observed on 18 June 1976 with a humpback whale located at lat. 42°09′N, long. 70°10′W, and with a fin whale located at lat. 42°04′N, long. 70°20′W, and on 20 June 1976 with a humpback whale located in the same general area (Northeast Fisheries Center[2]). During these three observations many herring gulls were again seen feeding at the surface and circling around the whales. Large numbers of American sand lance were also visually observed at the surface by NEFC personnel aboard the Alpine Geophysics RV *Atlantic Twin* and in the water column again by NEFC personnel aboard the General Oceanics research submersible *Nekton Gamma*. These latter two vessels were involved in testing the feasibility of using a research submersible to survey marine organisms (Northeast Fisheries Center[3]).

Bigelow and Schroeder (1953) reported that fin whales were observed feeding on American sand lance that were abundant in Cape Cod Bay in 1880. Nemoto (1959) listed American sand lance as one of the food items of baleen whales of the North Pacific, along with a variety of other fishes and euphausids. Fin and humpback whales are reported to feed on capelin, *Mallotus villosus*, a fish similar to the American sand lance in size, summer habitat, and schooling behavior in the continental shelf waters off Nova Scotia and Newfoundland (Mitchell 1974a). Fin whales landed at Blandford, Nova Scotia, from 1967 to 1972 contained sand lance (May-August), and stomachs from Newfoundland fin whales had >1% sand lance (June-July) in 1970-1972 (Mitchell 1974b). There is little stomach analysis data, though, from baleen whales captured in New England waters in the late 1880's when whaling was popular (True 1904), and no such data since the early 1900's when, for all practical purposes, whaling had ceased. Thus, it is difficult to confirm exactly what fin and humpback whales in the Cape Cod region eat.

The feeding observations which we made imply that the rorqual whales off New England, particularly fin and humpback whales, may be utilizing the high standing stock of American sand lance that is currently available (Northeast Fisheries Center[4]). Additionally noteworthy is that the Atlantic herring, *Clupea h. harengus*, a commonly mentioned rorqual whale food (Allen 1916; Ingebrigtsen 1929; Bigelow and Schroeder 1953; Nemoto 1959), is in low abundance at this time (International Commission for the Northwest Atlantic Fisheries 1976).

[1]Northeast Fisheries Center. 1977. Cruise Results, NOAA R/V ALBATROSS IV. Cruise No. 77-02, Spring Bottom Trawl Survey: Part III. Woods Hole, Mass., 6 p.

[2]Northeast Fisheries Center. Gulf of Maine whale sighting network reports. Groundfish Survey Unit. Data on file, Woods Hole, Mass.

[3]Northeast Fisheries Center. 1976. Cruise Results, R/V Atlantic Twin, Cruise 76-01. Woods Hole, Mass., 8 p.

[4]Northeast Fisheries Center. Spring groundfish survey research cruises 1967-1977. Groundfish Survey Unit. Data on file, Woods Hole, Mass.

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ESTIMATION OF INTERTIDAL HARVEST OF DUNGENESS CRAB, *CANCER MAGISTER*, ON PUGET SOUND, WASHINGTON, BEACHES[1]

There are two major methods employed in the sport fishery for the Dungeness crab, *Cancer magister*, in Puget Sound, Wash. The first is a passive method. A baited pot, trap, or ring net is placed on a subtidal substrate, left for a period of time, and retrieved. The second is an active method. During periods of low minus tides, sport crabbers seek crabs by sight. The crabbers usually wade out into water between knee and waist level, then walk parallel to the beach. A round metal loop, about 1 ft in diameter, covered with wire mesh and attached to a long handle, is generally used to capture crabs. Beginners often bring fish nets, but find it difficult to extricate the crabs caught in the net. When a crab is seen, the crabber maneuvers the hoop quickly under the crab. The crab's legs go through the mesh, making escape difficult, and the hoop is then pulled from the water. Only male crabs may be taken, and they must be a minimum of 152 mm (6 in) in width, as determined by a caliper measurement across the carapace, directly in front of the 10th anterolateral spines. The daily crab catch is limited to six per person.

Knowledge of the size and distribution of the intertidal sport fishery was limited until 1969, when the Washington Department of Fisheries began aerial surveys to estimate low tide usage of Puget Sound beaches for clam digging and crabbing. By summer 1973, enough data had been collected to show which beaches were being used for crabbing. However, the aerial surveys did not reflect the total use of beaches by crabbers over the entire low tide period, since only a single count was made sometime between 90 min before and 90 min after low tide.

This study was initiated in fall 1973 in an effort to determine the availability of crabs and the magnitude of intertidal harvest on one high-use Puget Sound beach. From data collected, an estimate was made of the total use of Puget Sound beaches by sport crabbers for daylight low tides in 1974.

Methods

From preliminary aerial survey data, Mission Beach, located 60 km north of Seattle and just beyond the Port of Everett, was selected as the study site (Figure 1). The beach is 3 km long, shallow, and sandy, with eelgrass beds below the mean lower low water (MLLW) level. This beach had only one public access, cut through a 15-m bluff. This location provided me with a good view of the entire area and made it possible to interview almost all crabbers using the beach.

From October 1973 to October 1974 there were 19 low tide series with tides lower than −0.30 m MLLW. These tidal series occurred in all months of the year except March and September. I visited Mission Beach during all tides lower than −0.30 m, except under adverse weather conditions in the winter months. I arrived 2.25 h before low water and walked to point 'a' (Figure 1), where I entered the water and moved toward the access at a depth of 0.15 to 0.85 m through the area most intensively utilized by the sport crabbers. For all crabs observed, I recorded the size to the nearest millimeter (taken in a horizontal measurement directly in front of the anterolateral spines on the carapace, by means of a caliper) and sex. Sampling was by the method used by most crabbers.

Beginning 2 h before low tide, I made half-hourly counts of the number of crabbers at the beach, but continued beach sampling of crabs until crabbers began to leave the beach, usually about 0.5 h before the low. At this time, I interviewed the crabbers about their success and time spent crabbing. About 90% of all crabbers using Mission Beach, on tides checked, were interviewed. During the interviews, I measured as many crabs as possible. From the interview data, I estimated the number of crabbers on the beach at any time during a period of 14 min before to 15 min after the half-hourly counts. The average time spent crabbing was slightly over 1.5 h; thus, if all crabbers

[1]Based on work submitted in partial fulfillment of the requirements for the degree of Master of Science.

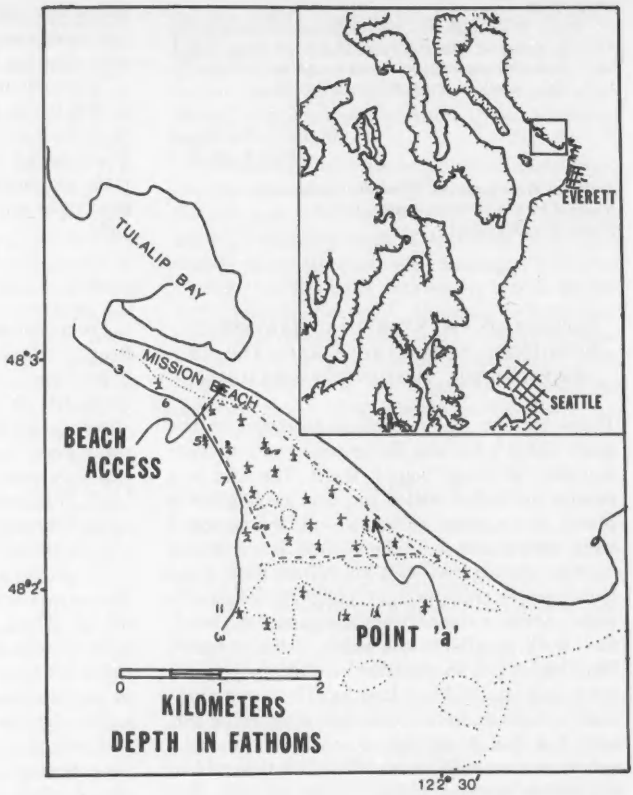

FIGURE 1.—Location of Mission Beach within Puget Sound, Wash. The area most intensively utilized by crabbers at Mission Beach is outlined with dashes.

had been interviewed, the constructed counts would coincide with actual beach use. However, not all crabbers were interviewed, so the half-hourly counts were more accurate for the lowest period of the tide when most people were crabbing.

I then constructed a table for each month which assigned the highest of the two estimates, either the constructed count from the interviews or the half-hourly beach count, to each half-hourly period. The number of crabbers using the beach was computed for each tide by dividing the total crabber hours (the sum of the half-hourly counts) by the average hours spent crabbing (obtained from crabber interviews) and totaled for each month. From the monthly table, the number of crabbers on the beach at any half-hourly interval, divided by the total number of people using the beach for each month during the low tide period, gave a percentage of people using the beach at any half-hourly count. Monthly use curves were then constructed for Mission Beach (Figure 2).

The methods that I employed to develop use curves were similar to those that have been used by researchers who have dealt with other recreational fisheries (Miller and Gotshall 1965; Brown 1969; Tegelberg[2]; Jarman et al.[3]).

In addition to the sampling that I conducted at Mission Beach, personnel from the Washington Department of Fisheries Shellfish Laboratory conducted creel sampling at six other Puget Sound beaches having differing levels of crabber use. From the survey material that they provided, I had insufficient data to construct use curves for

[2]Tegelberg, H. C. 1963. The 1962 razor clam fisheries. State Wash. Dep. Fish., 28 p.

[3]Jarman, R., C. Bennet, C. Collins, and B. Brown. 1970. Angling success and recreational use of twelve state owned lakes in Oklahoma. Paper given at 21st Annu. Meeting South. Div. Am. Fish. Soc., New Orleans, La.

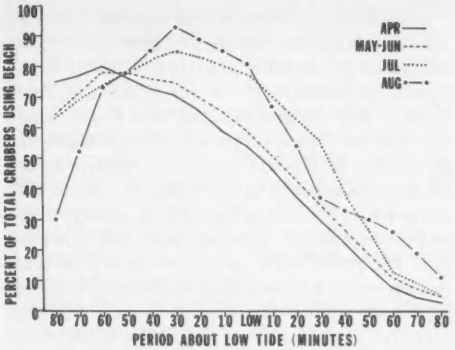

FIGURE 2.—Crabber use curves for Mission Beach based on data gathered April-August 1974.

April and August, but I was able to construct use curves for May-June and July, a combined total for those beaches based on 10 and 5 observations, respectively. These use curves, when superimposed over the corresponding Mission Beach use curves, did not vary by more than approximately 10% for the period before, or 20% for the period after, the low tide.

The Washington Department of Fisheries also provided me with data from aerial surveys conducted over Puget Sound beaches on 27 April, 25 May, 22 June, and 20 July 1974. Most of the beaches were surveyed during the hour preceding the low tide, which corresponded to the highest beach use. Thus, the curves derived for Mission Beach were used for estimates for all beaches.

While interviewing crabbers at Mission Beach, it appeared to me that both the tidal height and tidal sequence were important factors in crabbing success. I therefore analyzed the data in two different ways. The various tidal series had from three to eight tides lower than −0.15 m (−0.5 ft). I divided the low tide heights into six levels by 0.15-m increments. The first minus tide of a series to fall into a tidal height category was defined as Tide One in the tidal sequence. Each succeeding tide was consecutively numbered, with the final tide in a series designated as the last minus tide to fall into a tidal height category. Thus, low tides of equal height from different tidal series were not always the same sequence number.

Results and Discussion

The number of crabbers using Mission Beach during the winter nighttime tides was small compared with the number during the summer daytime tides. Of the estimated 762 crabbers using Mission Beach during the year, only 27 (4%) crabbed from October through February, while 735 (96%) crabbed from April through August. Of the estimated 531 crabs taken for the year at Mission Beach, the winter crabbers caught 60 (11%), while the summer crabbers caught 471 (89%).

Stepwise multiple linear regression analysis (Poole 1974) of crabber activity at Mission Beach correlated significantly ($P<0.05$) with tide height, day of week, month, temperature, and wind velocity (Table 1). However, the resultant equation was not strong enough for predictive purposes. The tide height accounted for the largest amount of the variability. The lowest three tide levels had two to four times as many crabbers as the highest three levels (Table 2). The other significant variables indicated the following: weekend use by crabbers per tide was 1.5 times greater than the average weekday use per tide; the average number of crabbers per tide was highest in April, May, and June, with the use dropping off considerably in July and August; there were more crabbers at higher air

TABLE 1.—Summary table of multiple linear regression between total crabbers at Mission Beach and nine independent variables. The resultant equation was significant at $P<0.001$ for all steps.

Step	Variable entered	Significance[1]	Mult. R	R^2	R	Overall F
1	Tide height	0.001	0.45	0.20	0.45	12.35
2	Day of week	.003	.59	.34	−0.27	12.37
3	Month	.005	.67	.45	−0.39	12.61
4	Temperature	.007	.73	.53	0.26	12.92
5	Wind velocity	.027	.76	.58	−0.06	12.37
6	Tide sequence	.078	.78	.61	0.08	11.39
7	Previous day's catch/crabber	.698	.78	.61	0.04	9.59
8	Precipitation	.769	.78	.61	−0.06	8.21
9	Cloud cover	.825	.78	.61	−0.13	7.14

[1]The α level of significance for each variable as it was entered in the equation.

TABLE 2.—Crabber use and catch taken on six different tide heights (mean lower low water) at Mission Beach, Wash., April-August 1974.

Tide height (m)	No. of tides sampled	Mean no. crabbers per tide	Mean no. of crabs caught	Mean catch legal crabs per crabber	Total legal crab catch
−0.15 to −0.29	6	6	1.4	0.2	7
−0.30 to −0.44	14	13	7.9	0.6	110
−0.45 to −0.59	16	9	6.1	0.7	92
−0.60 to −0.74	6	19	24.7	1.3	173
−0.75 to −0.89	4	25	15.0	0.6	62
−0.90 to −1.04	5	27	5.4	0.2	27

temperatures, but this corresponded with the lowest tides in June, which occurred at midday; on days with high winds there were few crabbers. This was probably due to a lowered chance of success because waves on the beach made crabs difficult to see.

The estimated use of the beach by crabbers corresponded with the daily availability of crabs on the beach that I observed by sample crabbing. This availability appeared to be affected by current and tide height. Two hours before low tide, the water level over the eelgrass portion of the beach, where most crabs were found, was generally >1 m. As the tide went out and the water became shallower, I observed few crabs in water <0.15 m deep. The current also appeared to have effects. When the tide approached its lowest level, the current became slack, at which time I observed few crabs. Even on days when a large number of crabs were active an hour before the low, few would be evident at low slack.

The monthly use curves enabled me to take a single aerial survey count of crabbers using a surveyed beach at any time during the low tide period and predict the total crabber use at the beach during the entire low tide period.

I adjusted the total calculated Puget Sound beach use by crabbers during the 1974 aerial surveys by two factors: the number of crabbers excluded because beaches were not surveyed and the improper identification of people as crabbers who were not actually crabbing. Between 1969 and 1973, at least one aerial survey at low tide was conducted over every Puget Sound beach, and all important crabbing beaches were identified. From this data I estimated that the 1974 aerial surveys included 95% of the crabbers and other recreationists on the beaches at any given low tide. At the same time 1974 aerial surveys were made over Mission Beach, I made actual counts of crabbers on the beach. The average overcount of crabbers by the aerial survey was 15.5%.

Total Puget Sound intertidal crabber use for all low tides from April through August was roughly estimated by dividing the total Mission Beach counts on the days of the aerial surveys, April through July, by the adjusted total Puget Sound beach count. The quotient was designated as the percentage of Mission Beach use relative to the adjusted total beach count (Table 3). Due to poor visibility on the day scheduled, no aerial survey was conducted in August, so I used averaged data from the preceding 4 mo. I estimated the total crabber use on all beaches for each month by dividing the percentage Mission Beach use of the total adjusted beach count into the total crabber use of Mission Beach for each month.

In order to estimate the total crabs caught in Puget Sound by intertidal sport crabbers, I needed to know whether the average catch over a low tide period at other Puget Sound beaches was the same as that at Mission Beach. Six other beaches in Puget Sound that had different levels of crabber utilization were sampled on a random basis by personnel from the Washington Department of Fisheries. Their levels of crabber use ranged from a few to 70 crabbers per tide. Four of the six beaches had three or more surveys, and these were compared with Mission Beach by Wilcoxon Rank Sum Tests (Hollander and Wolfe 1973). The four beaches had W values of 13.5, 9.5, 46.5. and 106, which in all cases were greater than the computed values of 6, 6, 39, and 66. Thus the null hypothesis that there were equal catches per crabber at the different beaches could not be rejected. This implies that the number of crabbers at a beach is self-regulating in that crabbers tend to adjust their level of effort to the rate of return, and that rates of return for all crabbers at different beaches remains fairly constant.

This same pattern of utilization was observed in the recreational trout fisheries in California lakes, where the angling effort adjusted proportionally to the numbers of catchable-size trout (Butler and

TABLE 3.—Estimate of the total monthly crabber use in the intertidal Dungeness crab sport fishery for Puget Sound beaches, April-August 1974.

Month	Adjusted total Puget Sound beach count on monthly aerial survey	No. of crabbers at Mission Beach on monthly aerial survey	Percentage Mission Beach use of total adjusted beach count (Col. 3 ÷ Col. 2)	Total crabbers at Mission Beach	Estimated total intertidal crabber use (Col. 5 ÷ Col. 4)
April	433	27	6.2	79	1,274
May	829	28	3.4	229	6,735
June	954	33	3.5	279	7,971
July	805	29	3.6	121	3,361
August	No observation		[1]4.18	27	646
Total				735	19,987

[1]Average of four previous months.

Borgeson 1965). Since the catches did not differ significantly, all beaches were treated together for predictive purposes. An estimate of the total crabs caught by intertidal sport crabbers for the daylight tides in 1974 was made by multiplying the average catch per effort for April, May, June, July, and August at Mission Beach (Table 4) by the estimated total number of crabbers (Table 3) for each month. The number of crabs caught per month increased throughout the spring, reaching a maximum of 5,099 in June. Few crabs were caught after July (Table 5).

When Spearman rank correlation coefficients were computed between a crabber's catch at Mission Beach and a number of independent variables (Hollander and Wolfe 1973), the most significant positive correlation was with the total time spent crabbing (Table 6). Crabbing was better in April-June than in July and August. The tide height and tide sequence were not significantly correlated with the catch per crabber at $P<0.05$, but were significant at $P<0.10$. The highest average catches were on tides ranging from −0.60 to −0.74 m (Table 2).

The higher tides make crabbing difficult, because crabbers have to wade into deeper water to get to the area where crabs are found. In the deeper water, crabs are less visible and the mobility of crabbers is impaired. The catches and number of crabbers arranged by tide sequence are shown in Table 7. The lowest tides of the year are generally four or five tides into a tidal series. The first low tides in the series have already allowed a fair amount of crabbing pressure on the beach, and many of the available crabs have been removed. Additionally, the combination of crabbers wading and less water over the beach on the previous low tides probably causes crabs to move to deeper water during the last low tides in a series.

The sex and size composition of crabs that I observed while sampling are shown in Figure 3. The numbers of legal males (152 mm and larger) include all crabs measured during crabber interviews.

TABLE 4.—Monthly crabber use and mean daily catch at Mission Beach, Wash., April-August 1974.

Month	Number of tides	Number of crabbers	Mean daily catch per crabber	Range of mean daily catches
April	5	79	1.76	0.4-3.0
May	11	229	.86	0.0-3.4
June	14	279	.64	0.0-2.2
July	14	121	.59	0.0-1.7
August	6	27	.30	0.0-0.5

TABLE 5.—Estimated total Dungeness crab sport catch in Puget Sound on intertidal beaches, April-August 1974.

Month	Mean catch per crabber at Mission Beach	Estimated total Puget Sound crabbers	Estimated total crab catch
April	1.76	1,274	2,242
May	.86	6,735	5,792
June	.64	7,971	5,099
July	.59	3,361	1,983
August	.30	646	194
Total		19,987	15,310

TABLE 6.—Spearman correlation coefficients between number of crabs caught per crabber and nine independent variables.

Variable	Correlation coefficient	Significance
Time spent crabbing	0.738	0.001
Month	−0.413	.002
Tide height	0.229	.055
Tide sequence	−0.222	.061
Wind velocity	−0.175	.113
Temperature	−0.105	.238
Precipitation	−0.092	.263
Time of low	0.054	.355
Cloud cover	0.010	.473

TABLE 7.—Crabber use and catch taken on different tide heights arranged according to the sequence in which they occurred in a low tide series at Mission Beach, Wash., April-August 1974.

Tide sequence	No. of tides sampled	Mean no. crabbers per tide	Mean no. of crabs caught	Mean catch legal crabs per crabber	Total legal crab catch
1	6	15	7.6	0.5	46
2	9	23	10.3	0.9	163
3	8	13	9.4	0.7	85
4	8	13	6.5	0.5	52
5	8	9	8.9	1.0	71
6	7	18	6.3	0.4	44
7	3	14	2.7	0.2	8
8	1	20	2.0	0.1	2

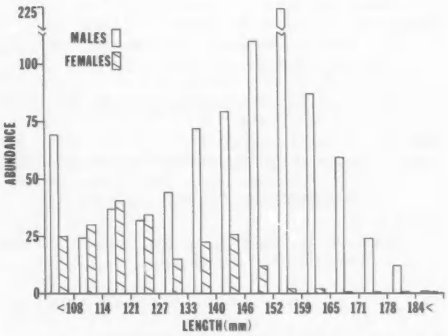

FIGURE 3.—Size composition and sex of crabs observed during sample crabbing at Mission Beach from October 1973 through August 1974. Male crabs >150 mm include those measured during crabber interviews.

In summary, the use of Mission Beach by intertidal crabbers is greatest 1 to 2 h before the low tide. This corresponds to the period when crabs are most readily observable. From the data collected at Mission Beach and aerial survey counts of other Puget Sound beaches, I estimated that about 20,000 crabbers utilized intertidal beaches from April through August 1974. The intertidal Dungeness crab sport fishery is, however, fairly small compared with other marine sport fisheries in Puget Sound.

Acknowledgments

I wish to thank G. Pauley, J. Congleton, C. Woelke, K. Chew, and T. Walker for discussion and critical readings of various stages of the manuscript. Reviewers for the *Fishery Bulletin* helped improve the readability. R. Whitney, as Leader of the Washington Cooperative Fishery Research Unit at the University of Washington, provided encouragement, support, and facilities from the outset of the study. Appreciation is extended to A. Scholz and other members of the Sport Shellfish Section of the Washington State Department of Fisheries, without whose cooperation this study would not have been possible. The study was partially supported by funds from the Washington Department of Fisheries.

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A CONTRIBUTION TO THE BIOLOGY OF THE PUFFERS *SPHOEROIDES TESTUDINEUS* AND *SPHOEROIDES SPENGLERI* FROM BISCAYNE BAY, FLORIDA

The general biology of the checkered puffer, *Sphoeroides testudineus*, and bandtail puffer, *S. spengleri*, is not as well known as that of the northern puffer, *S. maculatus*. For example, Chesapeake Bay populations of the northern puffer have been examined for length-weight relationships by Isaacson (1963) and Laroche and Davis (1973), for age, growth, and reproductive biology by Laroche and Davis (1973), and for fecundity by Merriner and Laroche (1977). None of this information is available on the checkered or bandtail puffer.

Checkered and bandtail puffers have greater geographic ranges and are more southern in distribution than the northern puffer. The checkered puffer is abundant from the Atlantic coast of southern Florida, throughout the Caribbean Islands, Campeche Bay, and along the coasts of Central and South America to Santos, Brazil (Shipp 1974). The bandtail puffer is common in the Caribbean Sea and along the coasts of peninsular Florida, the Bahamas, and Bermuda (Shipp 1974). I report here on growth, reproduction, and the pharyngeal dentition of these two species gathered during a study of their feeding biology (Targett 1978).

The sampling habitat was a shallow seagrass bed along the southwestern shore of Virginia Key in northern Biscayne Bay, Fla. Turtle grass, *Thalassia testudinum*, was the dominant seagrass with small amounts of shoal grass, *Halodule wrightii*, and manatee grass, *Syringodium filiforme*, also present. Monthly collections from September 1973 to December 1974 yielded 414 checkered puffers (15-215 mm SL; 56% females) and 548 bandtail puffers (16-133 mm SL; 49% females). Seawater temperatures ranged from 16.5° to 32.0°C and salinities from 30.5 to 38.5‰.

Standard length-weight relationships (Figures 1, 2) were calculated using functional regressions (Ricker 1973). Checkered puffers grow to a larger size and are heavier than bandtail puffers at a given length. Comparisons of these results with those for northern puffers from Chesapeake Bay (Isaacson 1963; Laroche and Davis 1973) was made possible by the conversion of total length to standard length using the factor: caudal fin length = 20.2% SL (Shipp 1974). Northern puffers grow

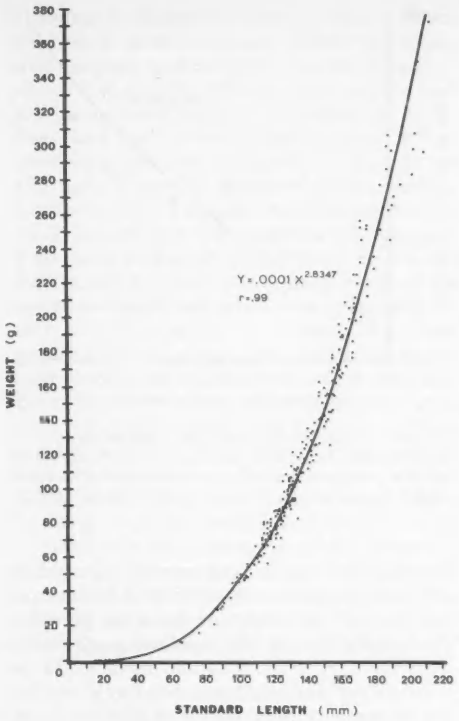

FIGURE 1.—Standard length-weight relationship for 250 checkered puffers from Biscayne Bay, Fla. Functional regression parameters derived by least squares fit to log transformed data, where variance about regression was $S_{y.x}^2 = 0.0014$.

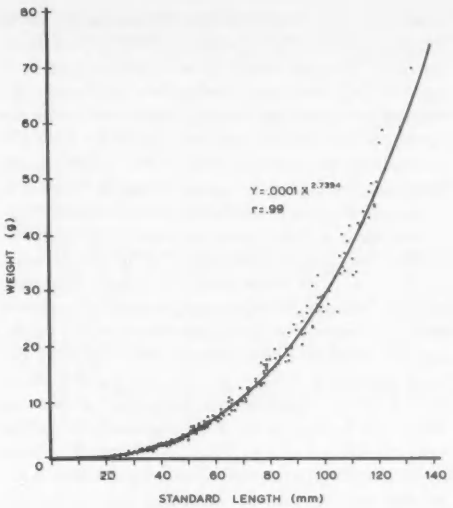

FIGURE 2.—Standard length-weight relationship for 250 bandtail puffers from Biscayne Bay, Fla. Functional regression parameters derived by least squares fit to log transformed data, where variance about regression was $S_{y.x}^2 = 0.0018$.

to a greater maximum size than either checkered or bandtail puffers and are approximately the same weight at a given length as checkered puffers.

Checkered puffers decreased in abundance in June and July due to a drop in numbers of 120-169 mm SL fish (Figure 3). (Some individuals may have left the seagrass bed as early as April and May, since a greater effort was needed to catch checkered puffers at that time.) Males and females decreased equally in abundance. The group leaving the seagrass bed may have been going elsewhere to spawn since their departure corresponded with the time of capture of ripe individuals. Some ripe checkered puffers were captured in April and May; and by August, September, and the beginning of October the few adults caught

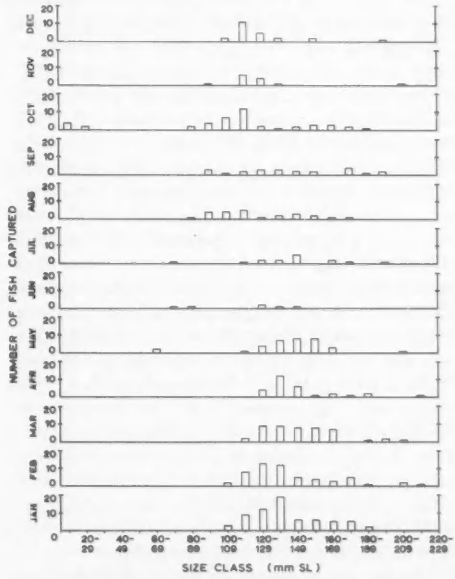

FIGURE 3.—Monthly standard length-frequency distributions for checkered puffers from Biscayne Bay, Fla., during 1974.

were all ripe. Furthermore, Christensen (1965) found evidence that checkered puffers from Jupiter Inlet, Fla., spawned in low salinity waters during the fall. He found young fish (≤10 mm SL) from early November through December in waters having salinities generally <20‰. He also observed that young and juveniles were abundant in the upper reaches of the Loxahatchee River (which flows into Jupiter Inlet) during winter and spring, rarely being found elsewhere. Thus, the checkered puffers leaving the seagrass bed in the present study may have been going to spawn in lower salinity waters found along portions of western Biscayne Bay or in the Miami River. This would explain why no checkered puffers <25 mm SL were captured, except for six in October. Most young likely remain in brackish water areas and move into higher salinity habitats only at larger sizes the following year. The 80-119 mm SL group appearing in August probably composed the 1-yr-old fish moving into the seagrass bed.

The checkered puffer spawning season, beginning in the spring and concentrated during summer and early fall in Biscayne Bay, occurs slightly later than the spring and summer spawning of the southern puffer, *S. nephelus*, at Cedar Key, Fla. (Reid 1954). The northern puffer in Chesapeake Bay has been reported to spawn during May by Hildebrand and Schroeder (1928) and during late May, June, and July by Laroche and Davis (1973).

Fecundity analysis, using the gravimetric technique, was done on nine checkered puffer females ranging from 127 to 178 mm SL (99-256 g). Only yolky eggs, with nuclei obscured, were counted. Regression analyses of fecundity-standard length and fecundity-body weight were done using functional regressions (Ricker 1973). Total fecundity increased exponentially as a function of body length (Figure 4) and linearly as a function of body weight (Fecundity = 1,431.81 [Body wt in grams] − 45,704.97; r = 0.96). Over the size range examined, relative fecundity averaged 1,146 eggs/g body wt. These fecundity values are greater than those found by Merriner and Laroche (1977) for northern puffers in Chesapeake Bay. Of the six checkered puffers <25 mm SL, two (15 and 23 mm SL) were males and the sex of the rest (17, 17, 18, and 21 mm SL) was undeterminable. Thus, it was not possible to estimate the body size at which eggs become discernible.

The age structure of the checkered puffer population can be inferred from the monthly length-frequency distributions (Figure 3). The 80-119 mm SL group appearing in August is likely 1-yr-old fish which grow to 120-189 mm SL by the end of their second year. A comparison of the growth of checkered puffers in this population with results from the work of Laroche and Davis (1973) on northern puffers from Chesapeake Bay shows that the checkered puffers reach a smaller size at the end of each year of life and are shorter lived than the northern puffers.

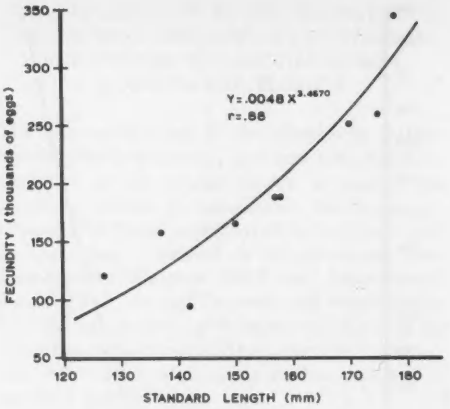

FIGURE 4.—Total fecundity-standard length relationship for nine checkered puffers from Biscayne Bay, Fla. Functional regression parameters derived by least squares fit to log transformed data, where variance about regression was $S_{y.x}^2 = 0.0078$.

Eggs became discernible, by microscope, in bandtail puffers at 25-30 mm SL. Spawning season, however, was not easily determined. No ripe or nearly ripe bandtail puffers were caught despite the fact that this species was abundant throughout the year and the full size range (to approximately 160 mm TL (Shipp 1974)) was captured. At least one fish <30 mm SL was collected every month except September, November, and December, although most were captured during March through June. This implies that bandtail puffers have a long spawning season, concentrated in the late fall and early winter, and spawn elsewhere with the young moving into the seagrass bed shortly after hatching.

Both checkered and bandtail puffers feed mainly on crabs, bivalves, and gastropods (Targett 1978). They use their beaklike jaws (paired premaxillary and dentary bones) to break the shelled prey. Two specimens of both species were cleared and stained, revealing that they have similar

pharyngeal dentition. Three pairs of dorsal pharyngeal tooth plates are present, associated with the pharyngobranchial elements of branchial arches I, II, and III, with one tooth plate of each pair being located on either side of the dorsal midline. Each tooth plate is slightly curved with a posteriorly directed dentigerous surface. In the 126- and 137-mm SL checkered puffers, the four tooth plates in the anterior two pairs were each 4 mm long and those in the posterior pair were each 3 mm long. In the 108- and 118-mm SL bandtail puffers, the four tooth plates in the anterior two pairs were each 3 mm long and those in the posterior pair were each 2 mm long. The dorsal pharyngeal tooth plates of both puffer species bear upon the pair of ventrally located, and nondentigerous, fifth ceratobranchial (lower pharyngeal) bones. The pharyngeal tooth apparatuses likely function to pull flesh from and to further grind and break crab and mollusc shells. The smooth puffer, *Lagocephalus laevigatus*, also has strong beaklike jaw teeth but has dentigerous tooth plates associated with the pharyngobranchial elements of only the II and III branchial arches (Tyler 1962). In general, fishes in the Order Plectognathi have very strong jaw teeth and comparatively weak pharyngeal dentition (Al-Hussaini 1947).

Acknowledgments

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CORRELATES OF MATURITY IN THE COMMON DOLPHIN, *DELPHINUS DELPHIS*

Maturity of the gonads in mammals is closely related to other aspects of physical development. Therefore, a simple method for estimating an individual's proximity to sexual maturity would be to evaluate appropriate morphometric data. However, the morphometrics traditionally collected on cetaceans are less than ideal for this task.

Studies on cetacean growth patterns have typically used data collected in a cross-sectional manner and have used large samples which included all age-classes. Unfortunately, individual rates and patterns are indistinct when values are averaged using this method (Sinclair 1973). If a large change in growth or development takes place over a short period of time and the beginning of this change does not occur at exactly the same age in each individual, the data acquired from a group of individuals will imply that the change takes place at a slower rate and over a greater period of time than is actually the case for an individual.

The present study used parameters which indicated the proximity of an individual to its own mature condition, not the average mature condi-

tion of the population. In *Delphinus delphis*, an individual's proximity to sexual maturity can be accurately assessed using appropriate morphometric data.

Materials and Methods

I used 35 male and 52 female *Delphinus delphis* specimens collected in southern California waters from 1971 to 1974.

The body weight in kilograms, body length in a straight line to the nearest centimeter from tip of the snout to the anterior portion of the fluke notch, dentine layers, bone development in the flippers, testes weights, and the numbers of scars on the ovaries were recorded.

Teeth were usually from the posterior one-third of the left mandibles; otherwise the largest teeth available were used. A longitudinal section 0.368 mm thick was cut from the center of each tooth, and samples were cleaned in a weak solution of ammonia. After rinsing with water, the sections were etched in 1-2% formic acid at room temperature until the dentine growth layers were distinct, usually 6-12 h. Sections were mounted on microscope slides in an ethanol solution and examined with transmitted light.

One light and one dark band were considered as one dentine layer. The interval for dentine laminar deposition is unknown for the *D. delphis* in the present study but I assume that the bands were laid down at regular intervals. *Delphinus delphis ponticus* Barabash of the Black Sea are reported to have two sets of alternating layers each year (Kleinenberg and Klevezal 1962).

Because different bones fuse at different times in the spotted, *Stenella attenuata*, and the spinner *S. longirostris*, porpoises (Perrin 1972), I used the development of the epiphyses and their fusion to the diaphyses of the flipper bones as the indicator for physical maturity of the specimens. Each flipper was assigned an index by scoring the degree of epiphyseal fusion visible in radiographs: 0 when no epiphysis had been formed; 1 when the epiphysis had been formed but had not started its fusion to the diaphysis; 2 when the epiphysis and diaphysis were in the process of fusing; and 3 when the epiphysis and diaphysis were fused. The distal ends of the radius, ulna, metacarpals, and phalanges of each flipper were scored (Figure 1). The

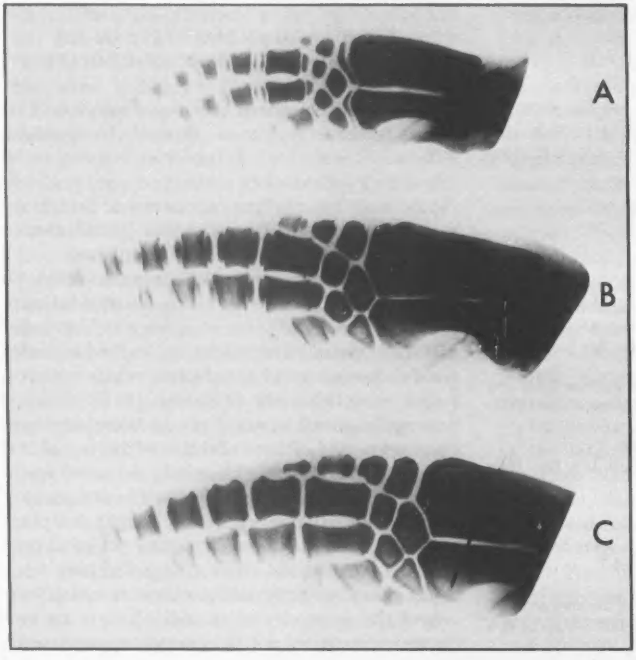

FIGURE 1.—Process of fusion of the epiphyses to the diaphyses in the flipper of *Delphinus delphis*. The flipper labeled A has a score (see text) of 18; B, 49; and C, 72.

sum of the individual epiphyseal fusion scores for both flippers composed the Flipper Index (FI) for that animal. When one of the flippers was damaged, the score for the undamaged flipper was doubled.

The combined weights of the testes with the epididymus removed were used as a measure of sexual maturity in males. In this study, a pair of testes was considered mature at 350 g.

Just as menarche in human females does not mean ovulation but the final developmental stages for the ability to ovulate, delphinid ovarian scars are here inferred to indicate ovulatory capacity. The presence on the surface of at least one corpus albicans or a corpus luteum indicated sexual maturity. However, each ovary also was sliced into sections 1 mm thick and examined for internal corpora.

All statistical tests are described in Sokal and Rohlf (1969).

Results

Development of right and left flippers did not differ significantly in 27 males and 55 females ($P \geq 0.05$, t-test for paired comparisons).

There was no significant difference ($P \geq 0.05$) in weight between the left and right testes of 34 specimens (t-test for paired comparisons).

In all but 2 of 25 mature cases, the left ovary had more scars.

Dentine layers are a poor indicator of sexual development in *D. delphis*. The numbers of dentine layers and ovarian corpora are not significantly related ($P > 0.10$, Kendall's rank correlation test). Both sexually mature and immature females occur with 7-14 dentine layers (Figure 2). Testes weights are so variable in the range of 7-12 dentine layers that they cannot be estimated (Figure 3), although significantly correlated over the entire range of data ($P \leq 0.001$, Kendall's rank correlation).

Body length is a poor indicator of sexual development. Over body lengths 175-190 cm, testes apparently undergo a transitional stage of growth. Gonad weight cannot be accurately estimated from body length over this range (Figure 4) although the two are significantly correlated over the entire range of data ($P \leq 0.001$, Kendall's rank correlation). Body length and ovarian scarring are poorly correlated ($P > 0.10$, Kendall's rank correlation). Body lengths 165-182 cm include both sexually mature and immature females (Figure 5).

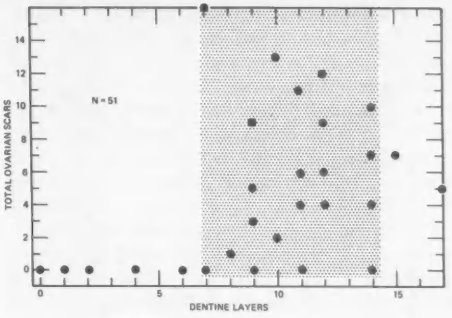

FIGURE 2.—Ovarian corpora in relation to dentine layers in *Delphinus delphis*. The stippled region indicates the range of dentine layers over which sexually mature animals are indistinguishable from immature.

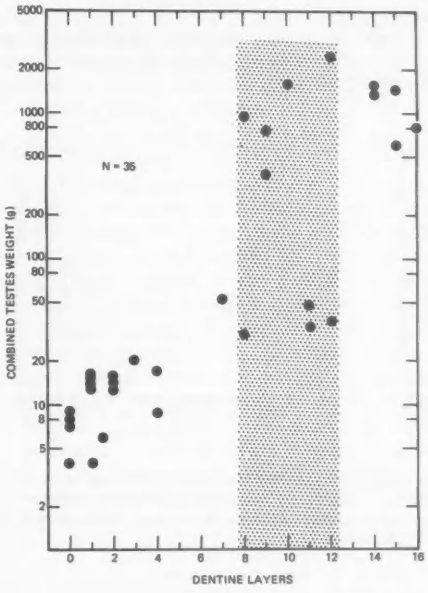

FIGURE 3.—Testis weight in relation to dentine layers in *Delphinus delphis*. The stippled region indicates the range of dentine layers over which testes of mature and immature weights overlap.

The FI is significantly correlated with testes weights ($P \leq 0.001$, Kendall's rank correlation) although data are missing in a narrow range (Figure 6). However, inactive ovaries occur in a wide

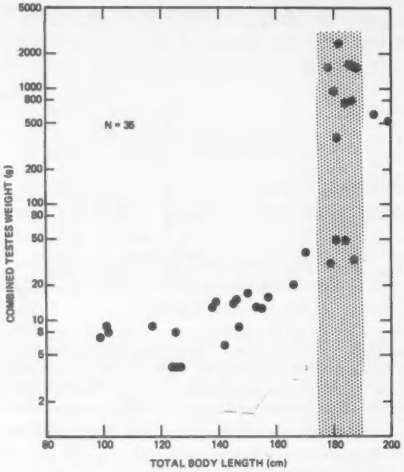

FIGURE 4.—Testes weights in relation to body length. The stippled area indicates the region of overlap for mature and immature testes weights.

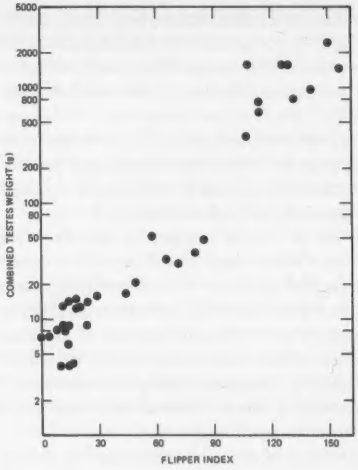

FIGURE 6.—Development of testes related to epiphyseal development of the pectoral appendages in *Delphinus delphis* as indicated by the Flipper Index. The best interpretation of the present data is that two linear phases are separated by a stage of rapid change.

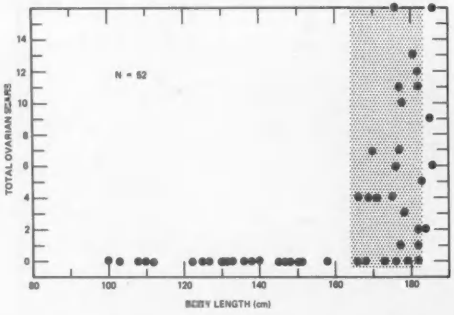

FIGURE 5.—Ovarian corpora related to body length in *Delphinus delphis*. The range of body lengths in which sexually mature and immature animals cannot be distinguished is indicated by the strippled area.

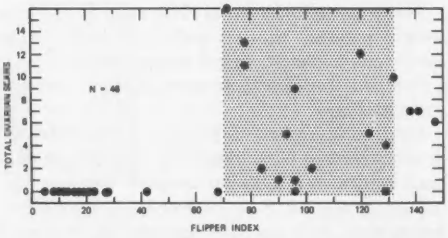

FIGURE 7.—Ovarian corpora related to pectoral epiphyseal development (Flipper Index) in *Delphinus delphis*. The shaded area indicates the range in Flipper Index over which sexually mature and immature animals overlap.

range of FI scores (Figure 7) and there is no significant relationship between the number of ovarian scars and the FI ($P>0.10$, Kendall's rank correlation).

Robustness is here defined as the body length in centimeters divided by body weight in kilograms. Regardless of body length, only the most robust individuals are sexually mature. Sexual maturity occurs when the male's length/weight ratio declines to about 2.6 (Figure 8). Mature females had length/weight ratios lower than about 3.0 (Figure 9). Of the 24 females with ovarian scars in this study, 16 were pregnant. Assuming the weight of the amniotic sack is nearly equal to that of the fetus, twice the weight of the fetus was subtracted from the gross weight of the mother, leaving the weight of the nonpregnant female for calculations of robustness. The robustness of the pregnant females is not separable from the sexually mature nonpregnant females.

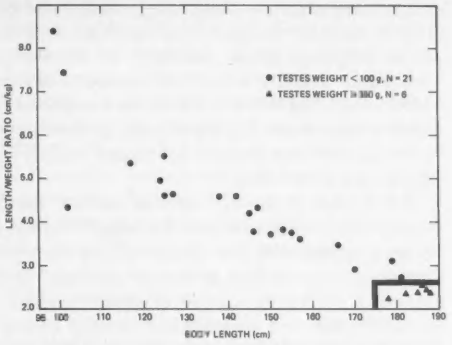

FIGURE 8.—The body length/weight ratio as related to body length in male *Delphinus delphis*. Individuals with combined testes weights of 350 g are considered to be undergoing spermatogenesis. The shading designates the weight/length ratio in which males apparently are sexually mature.

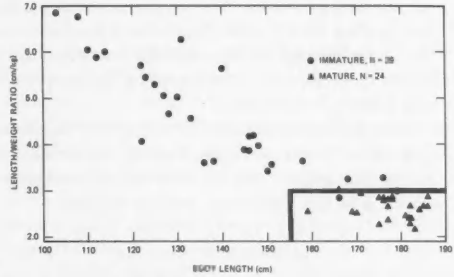

FIGURE 9.—Relationship of the body length/weight ratio to body length in female *Delphinus delphis*. Triangles represent individuals with at least one ovarian corpus. The shaded area denotes length/weight ratios in which sexually mature dolphins predominate.

Discussion

The data indicate that sexual development is better correlated with parameters which indicate the individual's proximity to physical maturity than with fixed morphometric values. A large increase in combined testes weight from <80 g to almost 400 g corresponds with rapid skeletal growth in the individual dolphin (Figure 6). Consequently, the FI is better correlated with sexual maturity in males than dentine layers or body length. Robustness is also highly correlated with sexual development in males but the sample size is small.

For unknown reasons, ovulation is better correlated with the length/weight ratio than with body length, dentine layers, or flipper bone development. Similarly, in studies of humans, it was found that girls who attained early menarche also had greater weight for height than their chronological peers who attained maturity at a later time (Simons and Greulich 1943). Data from *S. attenuata* (Perrin et al. 1976) also show ovarian corpora to be poorly correlated with age and length.

Induced ovulation is a distinct possibility for *D. delphis*. Harrison and Ridgway (1971) concluded that ovulation in *Tursiops truncatus* is induced but the mechanism is unknown. The present data imply that some *D. delphis* females never ovulate, supporting the findings of Harrison et al. (1972).

Oliver's[1] examination of *Delphinus* from the eastern tropical Pacific showed that the smallest testes with spermatogenesis weighed 140 g. For the present study, specimens with combined testes weights >350 g were collected in March, April, July, September, October, November, and December. The large testes weights throughout the year indicate that there is no seasonal rut, supporting the findings of Harrison et al. (1969).

Gaps in the data occur immediately prior to male *D. delphis* sexual maturity: FI scores 85-105 (Figure 6), body lengths 158-177 cm (Figure 4), 4-8 dentine layers (Figure 2). These gaps appear to be the prepuberty ranges for those indicators. Behavior patterns may account for the absence of data in these regions. Young males of *Physeter catodon* (Ohsumi 1971) and *Tursiops truncatus* (Evans and Bastian 1969) frequently herd separately from the rest of the population. Alternatively, these animals may have a greater capacity to escape nets. Female specimens also are lacking in the length, age, and FI ranges just prior to the demonstration of ovarian scars. Preadolescent females, like the males, may easily escape nets, or have a social structure separate from the main herd.

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[1]C. W. Oliver, Inter-American Tropical Tuna Commission, La Jolla, CA 92037. Unpubl. data.

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LARVAL DEVELOPMENT OF *GOBIESOX RHESSODON* (GOBIESOCIDAE) WITH NOTES ON THE LARVA OF *RIMICOLA MUSCARUM*

Seven species of clingfishes of the genera *Gobiesox* and *Rimicola* occupy the rocky inter- and subtidal areas along the California coast. Extreme modification of the pelvic fins into a suction disc enables them to cling to rock and algal substrates. Although all clingfish species are listed as being uncommon to rare in California by Miller and Lea (1972), clingfish larvae are collected on a regular basis (although in low numbers) by monitoring programs dealing with fish larvae (Brewer,[1] McGowen,[2] and White[3]). Of the seven species recorded in southern California, adults of only two, *G. rhessodon* and *R. muscarum*, are usually encountered (pers. obs.).

Knowledge of larval stages of eastern Pacific (especially Californian) fishes is largely limited to pelagic species of those coastal species with protracted pelagic larval periods (Ahlstrom 1965; Moser et al. 1977). Larvae of many nearshore, coastal fishes are undescribed. Recent concern over the affects of harbor development and thermal discharge and entrainment from power plants on fish populations has intensified the need for proper identification of fish eggs and larvae.

The principal systematic work to date on the adults of eastern Pacific clingfishes was carried out by Briggs (1955). No previous works on the larvae of eastern Pacific clingfishes have been carried out, although the eggs and larvae of an Atlantic clingfish, *G. strumosus*, are well known (Runyan 1961; Dovel 1963).

Descriptions of a larval series of *G. rhessodon* and early larvae of *R. muscarum* are presented here as taxonomic aids to larval fish investigators working in the California coastal region.

Methods and Materials

Eggs and adults of *G. rhessodon* and *R. muscarum* were collected in June 1977 from the intertidal zone at low tide at Catalina Harbor and Little Harbor, Santa Catalina Island, Calif. Adults with their eggs were transported to the Catalina Marine Science Center (CMSC) operated by the University of Southern California and maintained in tanks with running seawater. The failure of hatched larvae to feed (probably due to lack of suitable food) precluded culturing past 2 days (4.0 mm). Additional specimens of *G. rhessodon* utilized in the series were obtained by vertical plankton tow under a night-light at the CMSC dock in Big Fisherman's Cove (4.7 mm) in June 1977; by horizontal tow in King Harbor, Redondo

[1]Gary D. Brewer, Institute for Marine and Coastal Studies, University of Southern California, Los Angeles, CA 90007. Pers. commun. June 1977.
[2]Gerald E. McGowen, Southern California Edison (Occidental College), Redondo Beach, Calif. Pers. commun. June 1977.
[3]Wayne S. White, U.S. Fish and Wildlife Service, Laguna Niguel, Calif. Pers. commun. August 1977.

Beach, Calif. (7.5 mm), in 1977; by otter trawl in Marina del Ray, Calif. (12.0 mm), in June 1977; and from the larval fish collection of the Harbors Environmental Projects (University of Southern California) taken by horizontal plankton tows in Los Angeles Harbor (specimens collected in 1972-73). A total of 32 larvae from 2.6 to 7.5 mm of *G. rhessodon* were examined for larval characteristics. An additional 311 larvae of *G. rhessodon* (2.9-7.5 mm) from King Harbor were checked specifically for the presence of melanophores on the head. Larvae were examined and drawn using a Wild[4] stereomicroscope fitted with a camera lucida. Standard length (SL) was measured from the tip of the snout to the tip of the notochord until completion of notochord flexion and then to the posterior margin of the hypural plate.

Results and Discussion

Gobiesox rhessodon

The most distinctive character of *G. rhessodon* larvae was the presence of 8-17 (mean 12) stellate melanophores, which ran laterally in two or three rows from the pectoral fin region to just posterior to the anus (Table 1, Figures 1-3). The dorsum of the gut was also heavily pigmented with stellate melanophores (not included in the lateral melanophore counts). The gut pigmentation often obscured the well-developed swim bladder. Myomere counts ranged from 24 to 29 (mean 27) but were difficult to count, especially in early stages. All specimens up to 6.9 mm had four to seven regularly spaced melanophores along the ventral portion of the tail region. The length of the gut averaged approximately 35% of body length in all specimens examined. Head length ranged from 19 to 25% SL in most specimens <6.5 mm. Individuals ≥6.5 mm had a much larger head of about 33% of SL. All specimens had a stellate melanophore at the base of each pectoral fin which was covered by the opercular flap in later stages (>6.9 mm). The larvae from Catalina and Los Angeles Harbor possessed from zero to four spots on the dorsal portion of the head. Forty-two percent (mean 24, range 2.6-6.9 mm) of the larvae had head pigmentation in the form of spots. Of the larvae examined from King Harbor, 79% (mean 311) lacked this head pigmentation. The larvae with and without head spots were very similar in every other respect.

The larvae of *G. rhessodon* hatched at about 4.0 mm (three specimens ranged from 3.9 to 4.1 mm) from attached, monolayered eggs laid under rocks and cobble in the intertidal zone at Catalina Island. Nest guarding adults have been found from spring to early summer by Lavenberg.[5] The relatively advanced larvae possessed well-developed jaws and pectoral fins at hatching and a laterally bilobed yolk, which was absorbed within the first 24 h. The gut had two or three constrictions giving it the appearance of being looped. The constrictions were characteristic of the larvae up to 6.9 mm. Notochord flexion occurred between 5.5 and 6.9 mm, and caudal fin rays started to develop just prior to flexion. Dorsal and anal fin ray development began around 6.2 mm and the fins were developed sufficiently for positive identification at about 6.9 mm. The development of the pelvic fins began at 5.5 mm and the characteristic suction disc was formed at about 7.0 mm. Transformation and settling probably occur between 8 and 12 mm as evidenced by an 8-mm planktonic specimen from King Harbor that possessed juvenile pigmentation (McGowen see footnote 2) and the 12-mm juvenile (Figure 3) which was collected by benthic otter trawl. This latter specimen exhibited the ability to cling to surfaces after capture.

Larvae of *G. rhessodon* appear to be the most common *Gobiesox* encountered in several nearshore plankton sampling programs in southern California (Brewer see footnote 1; McGowen see footnote 2; White see footnote 3). This is to be expected in that previous species lists of adult/

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of larval measurements and adult counts for *Gobiesox rhessodon* and *Rimicola muscarum* (Miller and Lea 1972 and present study).

Item	*Gobiesox rhessodon*	*Rimicola muscarum*
Larvae:		
No. lateral melanophores	8-17 ($\bar{x}$ = 12) in 2-3 rows	40-50 in 4 rows
Myomere count	24-29 ($\bar{x}$ = 27)	[1]
No. ventral tail melanophores	4-7	Absent
Size (mm) at onset of pelvic fin development	5.5	?
Adults:		
No. visible dorsal fin rays	10-12	6-8
No. visible anal fin rays	9-10	6-8
No. pectoral fin rays	19-21	14-17
No. vertebrae	[2]28-29	[2]35-36

[1]Lateral melanophores obscurred myomeres so that accurate counts could not be taken.
[2]Counts from Los Angeles County Museum specimen X-rays—*G. rhessodon* (LACM 1998), four specimens; *R. muscarum* (LACM W70-16), six specimens.

[5]Robert J. Lavenberg, Curator of Fishes, Los Angeles County Museum of Natural History, Los Angeles, CA 90007. Pers. commun. June 1977.

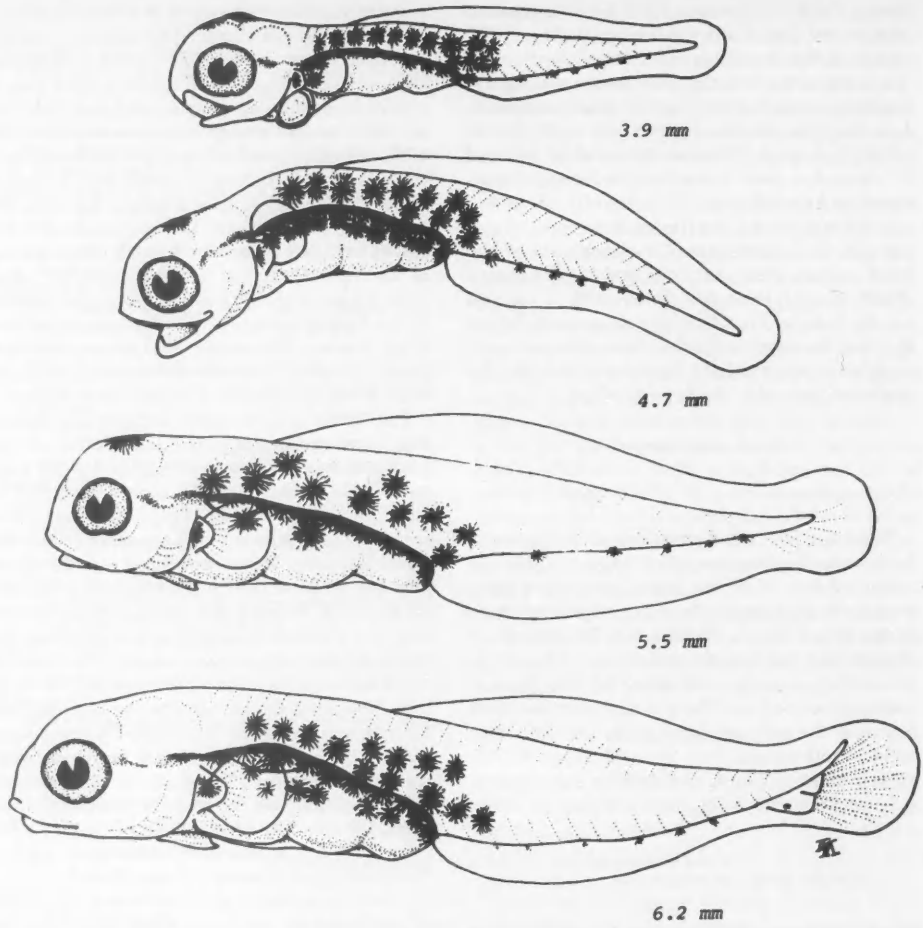


FIGURE 1.—Developmental stages of *Gobiesox rhessodon*. The 3.9-mm larva was reared in the laboratory (<24 h). The remainder are from plankton collections.

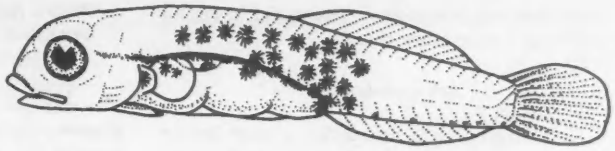
juvenile fishes in southern California coastal areas have included *G. rhessodon* exclusively (Horn and Allen 1976).

Rimicola muscarum

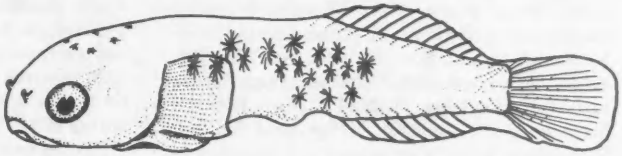
Yolk-sac larvae of *R. muscarum* (Figure 4), shortly after hatching, can be distinguished from *G. rhessodon* larvae at this stage by the greater number of lateral, stellate melanophores (40-50) in four rows that continue to the sixth or seventh postanal myomere, and the absence of pigmentation on the ventral tail region (Table 1). Yolk-sac larvae do not have head pigment. Adult counts are also markedly different from *G. rhessodon* (Table 1).

Comparison

Three species of *Gobiesox*, in addition to *G. rhessodon*, have been reported in southern California: *G. maendricus*, *G. papillifer*, and *G. eugrammus*.

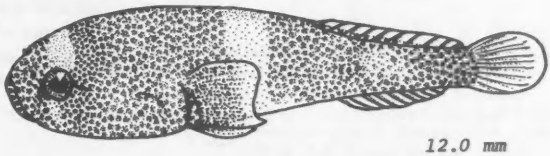


6.9 mm



7.5 mm

FIGURE 2.—Pelagic larvae of *Gobiesox rhessodon*.



12.0 mm

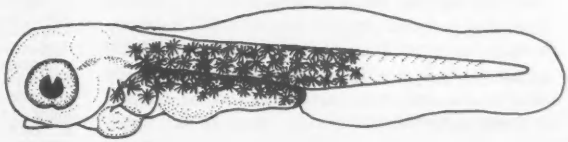
FIGURE 3.—Late pelagic larva (upper) and benthic juvenile (lower) of *Gobiesox rhessodon*.

The larval stages of *G. maeandricus* have recently been described by Marliave (1976). Based on Marliave's description and data from Richardson,[6] *G. maeandricus* larvae differ from *G. rhessodon* mainly in that *G. maeandricus* lack lateral melanophores and possess more myomeres (31-33). In addition, adults of *G. maeandricus* are rare south of Point Conception, Calif. (Miller and Lea 1972). *Gobiesox papillifer* and *G. eugrammus* are also rare in southern California. *Gobiesox papillifer* has been reported only once in southern California, and *G. eugrammus* only ranges as far north as San Diego County (Miller and Lea 1972). The larvae of these two species of *Gobiesox* have not been described, however, it is unlikely that any of these forms were among the specimens examined considering the distributions of the adults.

The Atlantic species of *Gobiesox*, *G. strumosus*, studied by Runyan (1961) and Dovel (1963) was similar in appearance to *G. rhessodon*, but does differ in that the Atlantic species had 10-15 saddle melanophores (as opposed to lateral) and displayed no ventral midline pigment in the early stages (<3.9 mm). Later larvae of *G. strumosus* also appeared to be more heavily pigmented on the trunk portion of the body (4.73-8.78 mm).

The presence or absence of head pigmentation has been used by some investigators to separate *Gobiesox* larvae collected in southern California into two types. This character is variable in *G.*

[6]Sally L. Richardson, School of Oceanography, Oregon State University, Corvallis, OR 97331. Pers. commun. May 1978.



4.0 mm

FIGURE 4.—Yolk stage larva of *Rimicola muscarum*.

rhessodon and, therefore, is not useful in distinguishing it from other species.

Acknowledgments

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SPRING AND SUMMER FOODS OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN THE EASTERN BERING SEA

The walleye (Alaska) pollock, *Theragra chalcogramma* (Pallas 1811), is the most abundant commercial fish species in the eastern Bering Sea (Pereyra et al.[1]) and plays an important role in ecosystem trophodynamics of the region. To obtain better knowledge of the role of the pollock as a predator, we have studied the stomach contents of pollock from the eastern Bering Sea collected on U.S. research vessels in the summer of 1974 and on Soviet and Japanese fishing vessels in the spring of 1977.

Results from this study contribute to our understanding of feeding habits; information on seasonal and size-dependent changes in feeding behavior are used to model interactions between species (trophodynamics), and to predict the influence of commercial fisheries on the abundance of populations in the eastern Bering Sea (Laevastu and Favorite[2,3]).

Methods

Pollock stomachs were collected by U.S. fisheries observers, on an opportunistic basis, aboard Soviet and Japanese motherships in the eastern Bering Sea. Samples were collected in the region of the continental shelf break in April and May 1977 (Figure 1, Table 1). The stomachs were removed, tied in cheesecloth, and preserved in dilute Formalin[4] (ca. 5%) and sent to the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, Wash., for analysis. Identifiable matter was separated by major taxa. Wet weight for each taxa was determined after blotting with paper towels. Uniden-

[1]Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Unpubl. manuscr., vol. 1, 619 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[2]Laevastu, T., and F. Favorite. 1976. Evaluation of standing stocks of marine resources in the eastern Bering Sea. Unpubl. manuscr., 35 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[3]Laevastu, T., and F. Favorite. 1976. Dynamics of pollock and herring biomasses in the eastern Bering Sea. Unpubl. manuscr., 50 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

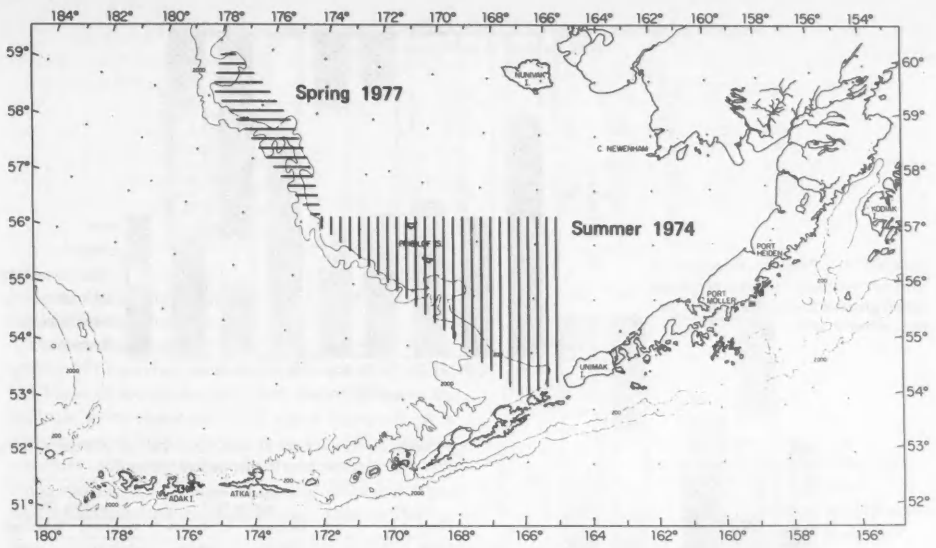

FIGURE 1.—Location sites where walleye pollock stomach samples were collected in the eastern Bering Sea.

TABLE 1.—Summary of walleye pollock stomach samples collected in the eastern Bering Sea.

Vessel	Sampling period	No. of stomachs collected	Depth range (m) of bottom	Average depth (m)
Oregon (U.S.)	July 1974	352	71-132	99
Chikubu Maru (Jpn.)	Apr. 1977	180	124-210	194
Tiraspol (U.S.S.R.)	Apr. 1977	225	128-256	167
Tenyo Maru #3 (Jpn.)	Apr.-May 1977	92	110-165	132
	Total	849		

tifiable matter was classed as "digested material" and also weighed. Percentage of food weight for each major food category, by fish-length group, was calculated as was the weight for each major food category per fish for each length group. Empty stomachs were not included in the analysis.

Detailed length data from foreign fishing vessels were available only from the Japanese fishing vessel *Tenyo Maru*. These data were analyzed by 10-cm fork length classes. Fish lengths from the Japanese fishing vessel *Chikubu Maru* and the Soviet fishing vessel *Tiraspol* were recorded only as greater or less than 35 cm (the approximate length at sexual maturity). This is also the size at which pollock become markedly cannibalistic (Takahashi and Yamaguchi 1972). Data from all three observer cruises were combined using these two major size categories to obtain sufficient sample sizes for comparison with the data collected in 1974.

Data collected in 1974 (RV *Oregon*) were examined by 5-cm length classes. The larger number of stomach samples collected during this cruise allowed a finer analysis of size-related changes in feeding habits. The methods used for processing samples from this cruise were approximately the same as for samples from the foreign vessels.

Results

An examination of stomach content weight by fish-length group provided evidence of related shifts in principal food categories in the diet of pollock (Figures 2, 3). In both spring 1977 and summer 1974, the percentage of copepods as food biomass tended to decrease with increasing size of pollock. The percentage of fish in pollock stomachs tended to increase with the size of pollock. Euphausiids were important food components in most length classes in both sampling periods. Amphipods, however, were only abundant in

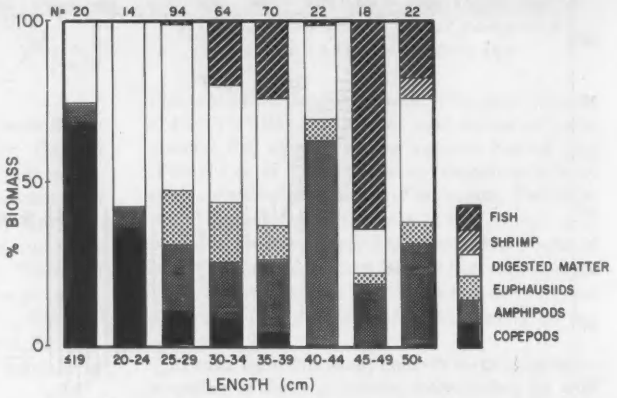

FIGURE 2.—Percent biomass of stomach contents by taxa per 5-cm length group of Bering Sea walleye pollock, summer 1974.

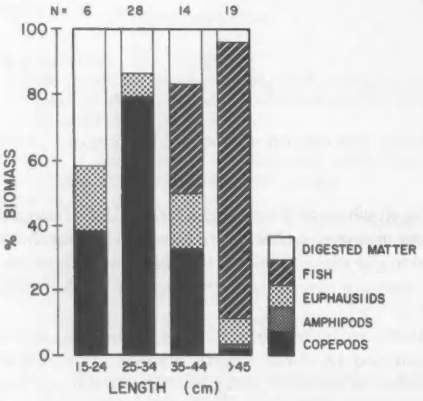

FIGURE 3.—Percent biomass of stomach contents by taxa per 10-cm length group of Bering Sea walleye pollock, spring 1977.

TABLE 2.—Proportion of taxa observed in walleye pollock stomachs in the eastern Bering Sea.

Taxa	Observer cruises, spring 1977		*Oregon* cruise, summer 1977	
	Weight (g)	% biomass	Weight (g)	% biomass
Fish	277.07	28.53	223.21	25.94
Copepods	349.81	36.02	44.60	5.18
Euphausiids	210.02	21.62	81.70	9.49
Amphipods	2.15	0.22	235.63	27.38
Chaetognaths	0.47	0.05	17.77	2.07
Cephalopods	0.30	0.03	—	—
Mollusks	0.15	0.02	0.89	0.10
Ostracods	0.02	—	—	—
Larvaceans	0.08	0.01	0.08	0.01
Annelids	3.99	0.42	3.40	0.40
Shrimp	12.91	1.33	9.79	1.14
Cumacean	—	—	0.01	—
Nemerteans	—	—	0.92	0.11
Mysids	—	—	0.55	0.06
Crab	—	—	4.56	0.53
Unidentified	—	—	1.64	0.19
Digested	114.09	11.75	235.83	27.40
Total	971.06	100.00	860.58	100.00

TABLE 3.—Grams of food organisms per fish (not including fish with empty stomachs) in each size class, *Tenyo Maru*, spring 1977.

Item	Fork length (cm) of pollock			
	15-24	25-34	35-44	>45
Grams copepods/fish	0.08	0.97	0.66	0.14
Grams euphausiids/fish	0.04	0.09	0.35	0.82
Grams fish/fish	—	—	0.69	5.28
Grams total food/fish	0.20	1.22	2.04	6.50
No. of fish with food	6	28	14	19
Percentage of fish with empty stomachs	57	26	18	17

stomachs collected in summer 1974, and the percentage of amiphods as food biomass tended to increase with increasing pollock size. Other food organisms that appeared in the diet are listed in Table 2.

The analysis of stomach contents by weight-percentage masks the behavioral aspects of pollock feeding due to size differences in food organisms. More information can be obtained from the data when analyzed as grams of food organisms per fish for each length class (Tables 3, 4). From this analysis it appears that larger pollock tended to exclude smaller food items from their diet. As the pollock grew larger they fed more on euphausiids, amphipods, and fish.

Data on the species composition of fish in pollock stomachs were available from the summer cruise of 1974 (*Oregon*). Fish ingested were identified from the stomachs of 27 pollock ranging in fork length from 26 to 57 cm (mean = 40 cm). Of the fish ingested, 89% by weight and 39% by number were

TABLE 4.—Grams of food organisms per fish (not including fish with empty stomachs) in each size class, *Oregon*, summer 1974.

Item	Fork length (cm) of pollock							
	<20	20-24	25-29	30-34	35-39	40-44	45-49	>49
Grams copepods/fish	0.42	0.26	0.14	0.16	0.13	0.02	—	—
Grams amphipods/fish	0.04	0.04	0.27	0.33	0.80	2.90	2.20	1.23
Grams euphausiids/fish	—	—	0.20	0.38	0.30	0.25	0.31	0.31
Grams shrimp/fish	—	—	—	—	0.01	—	—	0.40
Grams fish/fish	—	—	0.01	0.40	0.73	0.02	7.18	0.71
Grams total food/fish	0.62	0.70	1.27	1.97	2.91	4.57	11.24	4.00
No. of fish with food	20	14	94	64	70	22	18	22
Percentage of fish with empty stomachs	35	0	7	2	4	8	14	4

pollock. Other fishes identified included gadids, cottids, hexagrammids, and zoarcids.

Pollock food composition in summer 1974 and spring 1977 can be compared although geographic locations of stomachs collected varied (Figure 4). Pollock were observed with more copepods as a percentage of food biomass in spring 1974 than in summer 1977. Amphipods were nearly absent from stomachs collected in spring 1974 but were an important food component in summer 1977.

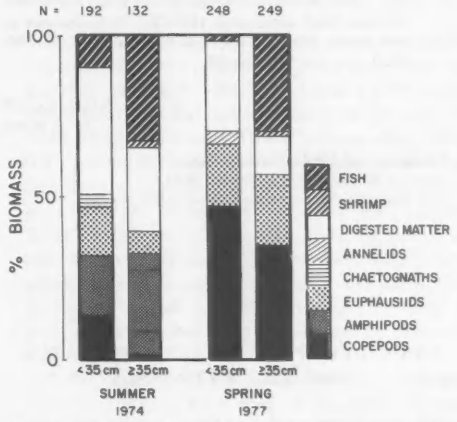

FIGURE 4.—Percent biomass of stomach contents by taxa for adult and juvenile walleye pollock in summer 1974 and spring 1977 in the Bering Sea.

Discussion

Previous studies on the food of the walleye pollock in the eastern Bering Sea indicated that in winter 1972, juvenile pollock fed mainly on euphausiids, while adult pollock fed on euphausiids, small pollock, and other fish (Mito 1974). In summer 1970, juvenile pollock fed on copepods and euphausiids, while adult pollock fed on euphausiids, small pollock, and other fish (Takahashi and Yamaguchi 1972). Our study indicates that in summer 1974 juveniles fed mostly on copepods, euphausiids, and amphipods, while adults fed on euphausiids, amphipods, and fish. In spring 1977, juvenile pollock fed mostly on copepods and euphausiids, while adult pollock fed on copepods, euphausiids, and fish. The results of these studies indicated that euphausiids are an important year-round food source of both juvenile and adult pollock. Fish appear to be an important year-round resource to adult pollock. The relative importance of other prey organisms in the diet of pollock seems to fluctuate between the studies.

Adult pollock tend to obtain a greater percentage of their food biomass from larger prey organisms than juvenile pollock, by ingesting more fish, euphausiids, and amphipods as they grow larger (Figures 2, 3). Additionally, larger pollock tend to exclude copepods from their diet (Tables 3, 4). These observations could result from an active process, based on preference or capture efficiency, or a passive process, resulting from spatial distribution.

Additional information is needed to understand the complexities of pollock feeding behavior, including: 1) seasonal variations in feeding behavior, 2) geographical variations, and 3) effects of alternate prey on cannibalism and grazing on other fish. This information would be useful in ecosystem modelling to understand the natural competitive and predatory interactions between fish populations and the potential effects of heavy exploitation.

Acknowledgments

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tifying the contents of fish stomachs collected in 1977.

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FECUNDITY OF THE ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

Although some work has been done to determine the time and place of spawning, age of spawning, and fecundity of Atlantic menhaden, *Brevoortia tyrannus* (Higham and Nicholson 1964), no attempt has been made to relate fecundity and age. In this study, I 1) examined the ovaries of fish 1 to 5 yr old collected during autumn 1970, in the vicinity of Beaufort, N.C.; 2) estimated the number of ripening ova in sexually mature fish; 3) calculated the mean number of ova spawned by fish of each age; and 4) determined the reproductive potential and the net reproductive rates for the 1954-63 year classes.

Atlantic menahden, family Clupeidae, constitute a single biological population (Nicholson 1972, 1978; Dryfoos et al. 1973) inhabitating coastal waters from Florida to the Gulf of Maine. It is subjected to an intensive purse seine fishery from Florida to New England. Fish are landed daily at reduction plants and processed into meal, oil, and solubles. Fishing begins in Florida and North Carolina in late April, in New Jersey coastal waters in early June, and in New England waters in late June. Fishing usually ends in mid to late November, except in the vicinity of Beaufort where schools of migrating fish of all ages from northern areas provide an intensive fishery from November to late December or early January.

Atlantic menhaden make extensive coastal movements and during the fishing season are stratified along the coast by age and size. In autumn most fish north of Virginia move southward and by January are concentrated in offshore waters from Cape Hatteras to northern Florida. About mid-March they begin a northward movement and by mid-June are stratified in coastal waters by age and size, the younger and smaller farther south and the older and larger farther north (Nicholson 1971). South of Cape Hatteras and in Chesapeake Bay most fish are ages 1 and 2. Age-2 fish dominate in coastal waters off New Jersey, ages 3 and 4 in Long Island Sound, and age 4 and older north of Cape Cod. Although they may live to age 9, few older than age 6 are caught.

Menhaden spawn in offshore coastal waters where the eggs hatch in 36 to 48 h (Reintjes 1962). Larvae, carried inshore by ocean currents, enter estuaries where they metamorphose to the adult form at about 35 mm total length. Although some spawning occurs in summer and early autumn in Long Island Sound and New England waters—the only areas where fish of spawning age are found during that time — most spawning occurs in the South Atlantic area from January to March and in the Middle Atlantic area from October to December and March to May. Although there appears to be only one spawning cycle each year, evidence is uncertain as to whether Atlantic menhaden are fractional spawners (Higham and Nicholson 1964).

As the population size decreased in the 1960's age structure also changed. Fish older than age 3 became extremely scarce, and most plants in the northern areas that were dependent on older fish closed. By 1969 few fish older than age 4 were landed, even in the North Carolina fall fishery. which traditionally had been dependent on older fish (Nicholson 1975).

Collection and Preparation of Ovaries

Ovaries were collected from 17 November to 29 December 1970 during the North Carolina fall fishery at the same time catches were being sampled routinely for age and size (June and Reintjes 1959). Sampling personnel measured and weighed the fish, removed scales for aging, and removed the ovaries. Only ripening ovaries fitting the

Stage III classification of Higham and Nicholson (1964) were retained. They were blotted on paper towels to remove excess moisture, weighed to the nearest 0.1 g, split longitudinally and turned inside out, and placed in individual jars of Gilson's fluid modified by Simpson (Bagenal 1967). The jars were shaken to liberate all eggs. After the Gilson's fluid was poured off, along with most pulverized ovarian tissue, the ova were washed and decanted in water several times and forced through a sieve to remove remaining fragments of ovarian tissue, spread on large trays covered with paper towels, and dried under incandescent lamps.

Higham and Nicholson (1964) described four stages in the maturation of ovaries. Ovaries in the immature and intermediate stages contain only undeveloped ova; ovaries in the maturing and ripe stages contain developing as well as undeveloped ova. They concluded that only maturing ova ripened during each spawning period. Maturing ova were described as being opaque and yellow and between 0.35 and 0.78 mm in diameter. I followed this description to separate immature from maturing ova. I also measured fecundity by estimating the number of maturing ova in both ovaries. Instead of counting ova in sample sections of the wet ovary, however, I counted ova in two replicate samples of the dried ova that had been separated from connective tissues. Before being weighed, eggs were allowed to equilibrate with air humidity. Each sample was weighed to the nearest 0.01 mg. If both ovaries weighed more than 12 g, two samples, each weighing 1/350 of the total weight, were taken. If the ovaries weighed 12 g or less, two replicate samples, each weighing 0.035 g, were taken, since fecundity would have been difficult to estimate in samples smaller than 0.035 g. Proportional sampling tended to minimize the counting error for a fixed amount of counting effort. Ova in each sample were counted under a stereoscope. The number of ova in both ovaries, N, was estimated by multiplying the number of ova in the two samples, N_s, by the ratio of total dry weight of eggs, W_t, to dry weight of eggs in samples, W_s ($N = N_s W_t / W_s$). To minimize counting error between samples, a coefficient of variation of 3.0% or less was maintained.

Preliminary calculations indicated that fecundity could be estimated with a precision of about 15% if 30 fish were selected randomly from each age-class. The ultimate number in each age-group was age 1, 21; age 2, 34; age 3, 33; age 4, 12; and age 5, 1 (Table 1).

TABLE 1.—Mean number of eggs (thousands) and mean ovary weight (grams), by age, for Atlantic menhaden sampled from the North Carolina fall fishery, 1970.

Age	No. of fish	Mean no. of eggs	Range	C.V.[1] (%)	Mean ovary wt	Range	C.V. (%)
1	21	115.8	26.5-250.7	47	17.9	4.0-43.5	54
2	34	177.4	39.2-368.8	50	30.1	5.0-62.5	55
3	33	302.8	127.7-458.3	30	50.9	21.1-96.9	34
4	12	308.6	142.7-514.0	36	48.5	22.0-74.8	36
5	1	568.4	—	—	90.0	—	—

[1]Coefficient of variation.

Fecundity

The regressions of fecundity on ovary weight, $F = 6{,}908(OW) - 17.937(OW)^2$, and fecundity on total fish weight, $F = 293(TW) + 0.214(TW)^2$, were curvilinear, but fecundity on body weight only, $F = 488(BW)$, was linear. The R^2 values were 0.981, 0.675, and 0.916, respectively. Although the relative merits of predicting fecundity from different variables are debatable (Bagenal 1967), these three models seem less useful than fecundity on age, which can be used to determine reproductive potential and calculate life table estimates, and fecundity on fish length, which can be used to predict the number of eggs spawned by different size classes.

A statistical test failed to support the curvilinear relation implied by a plot of fecundity on age, perhaps because of the few fish in older age-groups. Of the two linear models tested for estimating fecundity at age, I selected $F = 92{,}592(\text{Age})$ as the better estimator ($r^2 = 0.879$; SE slope = 3,440; SE regression = 89,110). It had tighter confidence limits and a higher r^2 than the model $F = a + bL$.

A logarithmic model ($\log F = a + bL$) was selected to describe the curvilinear relation between fecundity and length and was fitted to both my data and the data of Higham and Nicholson (1964) (Figure 1). Values predicted by this model fit observed values more closely over the entire range than those predicted by the nonlogarithmic model ($F = b_1 L + b_2 L^2$). The difference in the slope coefficients of the logarithmic model fitted to the two sets of data was significant ($P < 0.001$). Estimated fecundities were in reasonable agreement for fish up to 275 mm, but diverged for large fish. For 350 mm fish the model fitted to Higham and Nicholson data predicted about 1.75 as many ova as the model fitted to my data.

Differences in fish ages or in the time of year fish were collected, or actual changes in fecundity might account for differences in estimates of ova

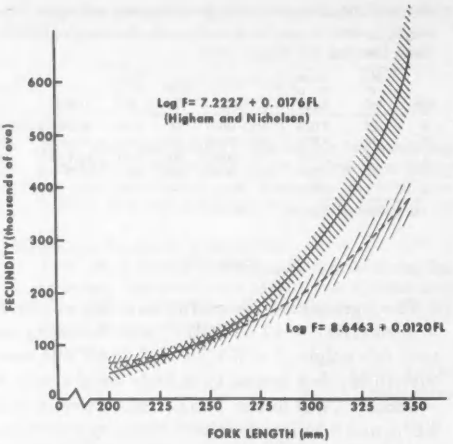

FIGURE 1.—Regression of fecundity on fork length for Atlantic menhaden showing confidence limits on the mean at 95% level. For $\log F = 7.2227 + 0.0176FL, N = 38$, SE regression = 0.3069; SE regression coefficient = 0.0011, $r^2 = 0.726$; for $\log F = 8.6463 + 0.0120FL, N = 101$, SE regression = 0.3330, SE regression coefficient = 0.0007, $r^2 = 0.871$.

for larger fish. Higham and Nicholson (1964), e.g., had four fish with between 400,000 and 500,000 ova, four with between 500,000 and 600,000, and one with over 600,000, whereas from nearly three times as many fish I had only two with over 500,000 and six with between 400,000 and 500,000. I believe, however, that differences in counting techniques caused the differences in ova estimates. I used proportional sampling, whereas they did not. I separated the eggs from each other and from the connective tissue, dried and weighed the eggs, and then counted those in a sample. They counted the eggs in a sample from the wet ovary. Also, a certain amount of subjectivity is involved in distinguishing between maturing and nonmaturing ova.

Reproductive Potential and Net Reproductive Rate

Since the sex ratio of Atlantic menhaden is about equal (Nicholson and Higham 1964), I was able to calculate the annual numbers of females of each age in the population, 1955-68, by dividing half of the number of fish caught at each age by the exploitation rate for all ages (Schaaf and Huntsman 1972). When I collected my material in 1970, recording the maturing stage of fish in catch samples had been discontinued, but Higham and Nicholson (1964) estimated that about 10% of age-1 fish, 90% of age 2, and 100% of age-3 or older fish examined during the North Carolina fall fishery in October-December from 1955 to 1959 had maturing ovaries. From these figures I calculated the number of females of each age that would spawn each year and multiplied it by the mean number of ova spawned by fish of each age to estimate the number of eggs spawned each year (Table 2).

The net reproductive rate, R_0, of a population is defined as the sum of the products of the age-specific survival rate l_x, and the age-specific natality rate m_x, of females (Odum 1971). A value of 1.0 for each generation would indicate that the population is stable and that there is a balance between births and deaths. In fish populations it is nearly impossible to obtain accurate counts or estimates of the number of offspring produced by each age-group. It is possible, however, to estimate the mean number of eggs spawned for fish of each age. If this variable is used for m_x in the formula given by Odum and if $\Sigma l_x m_x$ is called, $R_0{}^*$, then the reciprocal of $R_0{}^*$ should be a rough estimate of the survival rate of female eggs, providing the population is approximately stable. Although the Atlantic menhaden population declined after about 1960, I think in view of the imprecise estimates of other parameters, that it can be assumed stable for the purpose of estimating egg mortality.

$R_0{}^*$ values were calculated for the 1954-63 year classes. I assumed a 0.65 survival rate up to age 1, which I divided into the estimated number of fish that were age 1 (Schaaf and Huntsman 1972) for an estimate of the number of fish at the postlarval stage. Since the sex ratio is equal, this number divided into the estimated number of fish surviving to each age (Schaaf and Huntsman 1972)

TABLE 2.—Estimated number of eggs (multiply by 10^{11}) spawned by Atlantic menhaden, by year and age.

Year	Age in years							
	1	2	3	4	5	6	7-9	Total
1955	83.0	377.6	723.2	119.5	43.6	8.7	3.5	1,359.1
1956	69.7	443.9	103.7	465.1	118.8	31.1	10.7	1,243.0
1957	106.9	136.6	166.7	127.2	144.9	19.7	6.0	708.0
1958	161.1	131.3	51.0	62.8	42.9	28.8	3.0	480.9
1959	73.0	599.2	85.9	40.7	53.0	23.4	10.6	885.8
1960	329.8	205.3	457.9	142.0	59.4	21.1	6.8	1,222.3
1961	44.8	1,938.4	51.2	104.6	12.7	4.3	1.5	2,157.5
1962	57.7	270.2	877.6	85.0	85.0	12.4	3.4	1,391.3
1963	42.2	143.8	88.0	136.6	34.0	13.0	2.6	460.2
1964	38.4	95.3	34.1	19.9	21.0	5.0	1.4	215.1
1965	32.2	108.0	28.2	5.6	4.7	3.4	0.4	182.5
1966	31.2	44.0	9.0	1.1	0.4	0.5	0.2	86.4
1967	20.5	101.1	11.8	1.5	—	—	—	134.9
1968	41.3	91.2	24.7	3.0	0.2	—	—	160.4

yielded age-specific-survival fractions (l_x) for females of each year class. R_0* for each year class ranged from 7,100 to 25,800 (Table 3). The reciprocal of these numbers, 0.000141 and 0.000039, respectively, indicate a survival rate ranging from 39 to 141 females, or 78 to 282 fish of both sexes, for each 1,000,000 eggs spawned.

Any estimate based in turn on a series of rather imprecise and arbitrary estimates must be viewed with caution, and this one is no exception. Yet it is in line with current knowledge that the survival rate of pelagic fish eggs is extremely low.

TABLE 3.—Net reproductive rates (R_0*) and their reciprocals ($1/R_0$*) for the 1954-63 year classes of Atlantic menhaden.

Year class	R_0*	$1/R_0$*	Year class	R_0*	$1/R_0$*
1954	16,546	0.000060	1959	22,297	0.000045
1955	7,109	0.000141	1960	10,120	0.000099
1956	25,932	0.000039	1961	14,073	0.000071
1957	11,850	0.000084	1962	11,024	0.000091
1958	21,856	0.000046	1963	11,181	0.000089

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ROLE OF LAND AND OCEAN MORTALITY IN YIELD OF MALE ALASKAN FUR SEAL, *CALLORHINUS URSINUS*

The annual commercial harvest of male fur seals has fluctuated widely and declined since the early 1950's. This has occurred despite a fairly stable harvesting regime and efforts to maintain the population near the level believed to be consistent with maximum sustainable productivity (Chapman 1961, 1964, 1973). Variations in early natural mortality are mainly responsible for these changes in the harvest of males which occurs at ages 2-5 yr (mostly 3-4 yr). Kenyon et al. (1954) and Chapman[1] emphasized that natural mortality between birth and age 3 yr is high and that most of it probably occurs during the first winter just after weaning.

This report gives estimates of male survival from natural mortality of pups on land and from the first 20 mo of life at sea, a total interval of approximately 2 yr. The importance of pup numbers and early survival rates in determining annual variations in abundance at age 3 yr is quantified also.

Methods

Data for survival estimates are in Table 1. The age composition of annual kills before 1950 cannot be determined accurately because an aging technique was not available until then (Scheffer

[1]Chapman, D. G. 1975. Methods of forecasting the kill of male seals on the Pribilof Islands. Background paper for the 19th Annual Meeting of the North Pacific Fur Seal Commission, 10 p. (Unpubl. rep.)

TABLE 1.—Estimated numbers of male pups (born, dead, and living at the time of migration) and age-specific commercial kill of males from the 1950-70 year classes on St. Paul Island, Pribilof Islands, Alaska.[1]

Year class	Number of pups (thousands)			Number killed at age				
	Born	Dead	Living	2	3	4	5	2-5
1950	225.5	26.7	199	855	40,656	15,365	332	57,208
1951	223.5	35.3	188	1,384	32,350	18,083	3,057	54,874
1952	219.0	20.4	199	1,735	30,773	31,410	675	64,553
1953	222.5	39.1	183	839	38,312	8,855	54	48,060
1954	225.0	48.1	177	2,918	23,473	5,599	554	32,544
1955	230.5	37.8	193	1,015	27,863	10,555	115	39,548
1956	226.5	49.4	177	885	10,671	2,762	532	14,850
1957	210.0	30.8	179	2,590	24,283	15,344	773	42,990
1958	193.5	15.6	178	1,977	48,458	14,149	1,587	66,171
1959	167.5	20.0	148	2,820	26,456	14,184	1,764	45,224
1960	160.0	31.4	129	1,619	14,310	10,533	1,240	27,702
1961	168.4	29.0	139	1,098	22,468	12,046	1,270	36,882
1962	139.2	22.6	117	2,539	19,009	12,156	1,287	34,991
1963	132.0	16.3	116	1,264	25,535	11,785	1,542	40,126
1964	142.5	10.8	131	3,143	26,991	13,279	1,469	44,882
1965	133.4	19.6	113	2,200	18,706	10,565	731	32,202
1966	150.0	10.7	138	1,673	17,826	11,548	1,338	32,385
1967	142.0	7.0	135	2,640	22,176	12,503	2,185	39,504
1968	117.5	12.6	105	1,725	12,888	14,932	721	30,266
1969	116.8	6.6	110	323	15,024	10,800	1,631	27,778
1970	115.8	10.3	105	916	16,337	15,533	1,402	34,188

[1]Sources for data in Table 1, and footnotes, are given below:
Pups born: 1950-60, table 112 from Chapman (1973); 1961-65 and 1969-70, table 14 from Marine Mammal Biological Laboratory (1971[a]); 1967-68, table 10 from Marine Mammal Division (1976[b]). A 1:1 sex ratio is assumed (Kenyon et al. 1954; H. Kajimura pers. commun.).
Dead pups: 1950-60 (except 1952), appendix table 39 from Marine Mammal Biological Laboratory (1961[c]); 1952, counts (from same source) on sample rookeries only, extrapolated to island total from average contribution of these rookeries to known totals in 1951 and 1953; 1961-69, table A-12 from Marine Mammal Biological Laboratory (1971). A 1:1 sex ratio is assumed (Kenyon et al. 1954; M. C. Keyes pers. commun.).
Living pups: Pups born less dead pups, rounded to nearest thousand.
Kill by age: 1950-56 year classes, table 1 from Marine Mammal Biological Laboratory (1961[c]); 1957-64 year classes, table 1 from Marine Mammal Biological Laboratory (1971); 1965-70 year classes, table 1 from Marine Mammal Division (1976[b]).

[a]Marine Mammal Biological Laboratory. 1971. Fur seal investigation, 1970. Unpubl. manuscr., 155 p. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, WA 98112.
[b]Marine Mammal Division. 1976. Fur seal investigations, 1975. Unpubl. manuscr., 115 p. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, WA 98112.
[c]Marine Mammal Biological Laboratory. 1961. Fur seal investigation, Pribilof Islands, Alaska. Unpubl. manuscr., 148 p. U.S. Fish Wildl. Serv., Bur. Commer. Fish.

1950). However, the average numbers of pups migrating from land and of seals harvested at age 3 yr are approximated for the 1920-22 year classes in order to include in the yield-pup relationship a data point for the relatively small pup population then present. It should be mentioned that basic data were not taken during 1925-46 from which to estimate annual pup production.

The 1920-22 averages are based on kill data from Lander and Kajimura[2] and on pup data from Kenyon et al. (1954). The average number of pups born annually on St. Paul Island during 1920-22 was approximately 150,700. Their mean mortality rate on land was 2.2%, so an average of about 74,000 male pups migrated to sea annually. Because the harvest always has been selective for animals the size of 3- and 4-yr-olds, these 1920-22 year classes contributed to the kills mainly in 1923-26. The annual average kill then was 14,300, of which about 9,100 were age 3 yr assuming the same average (64%) as in the kills from the 1950-70 year classes (Table 1).

The kill of 3-yr-olds is used as an index of abundance at that age. The assumption is justified reasonably well by the generally stable harvesting regime and the usual predominance of this age group in the kills.

Annual population monitoring and behavioral data (Bartholomew and Hoel 1953; Peterson 1968) show the median date of birth on St. Paul Island is about 8 July, pup mortality on land is essentially over by mid-August, and the median date when pups migrate to sea is around 1 November. Survival of pups on land is calculated as the ratio of living pups to pups born (Table 1).

Few seals haul out on land until 24 mo of age, and survival is estimated for the first 20 mo at sea. These ocean survival rates are calculated from the data for living pups and age-specific kills (Table 1) and from the model of Lander (1975) with time intervals appropriately modified.

Results

Figure 1 shows wide fluctuations in the kill at age 3 yr around the regression line for pups born. After the effects of pup mortality on land are removed, high variability persists around the line

[2]Lander, R. H., and H. Kajimura. 1976. Status of northern fur seals. Food and Agriculture Organization of the United Nations, Scientific Consultation on Marine Mammals, Bergen, Norway, August 31-September 9, 1976, 50 p. (Unpubl. rep.)

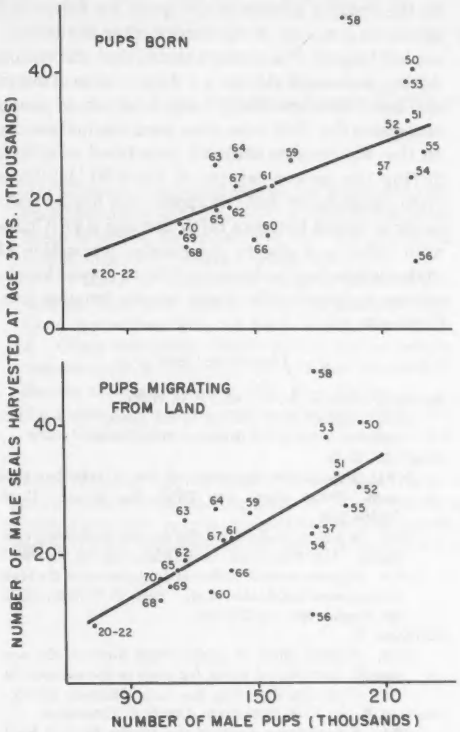

FIGURE 1.—Yield-pup relation for male fur seals of the 1920-22 and 1950-70 year classes from St. Paul Island. Least squares regression lines are shown for pups born ($a = 2.341$, $b = 0.126$) and for pups migrating from land ($a = 3.740$, $b = 0.188$).

TABLE 2.—Estimated natural survival rates of male fur seals from St. Paul Island in two stages from birth to age 2 yr, 1950-70 year classes.

Year class	Pups on land	First 20 mo at sea until start of kill at age 2 yr	Birth to age 2 yr
1950	0.88	0.41	0.36
1951	0.84	0.42	0.35
1952	0.91	0.46	0.42
1953	0.82	0.38	0.31
1954	0.79	0.30	0.24
1955	0.84	0.33	0.28
1956	0.78	0.18	0.14
1957	0.85	0.37	0.31
1958	0.92	0.49	0.45
1959	0.88	0.43	0.38
1960	0.81	0.34	0.28
1961	0.83	0.39	0.32
1962	0.84	0.43	0.36
1963	0.88	0.47	0.41
1964	0.92	0.47	0.43
1965	0.85	0.41	0.35
1966	0.92	0.36	0.33
1967	0.95	0.42	0.40
1968	0.89	0.42	0.37
1969	0.94	0.38	0.36
1970	0.91	0.46	0.42
All	0.87	0.40	0.35

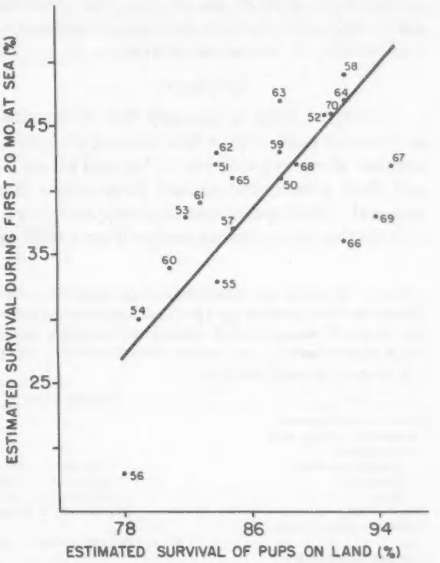

FIGURE 2.—Relation of estimated survival rate during first 20 mo at sea to estimated survival rate of pups on land for male fur seals of the 1950-70 year classes from St. Paul Island. Functional regression line shown (Ricker 1973) has intercept $u = 0.830$ and slope $v = 1.425$.

for pups migrating from land. Most of the variation in abundance at age 3 yr is evidently due to changes in the ocean survival rate undergone by the different year classes, not to changes in the rate of pup survival on land.

Estimated survival rates for the 1950-70 year classes are in Table 2 (ocean survival could not be estimated for the 1920-22 year classes without age composition data). The means and ranges of survival estimates in Table 2 are 87% (78-95%) for pups on land, 40% (18-49%) for the first 20 mo at sea, and 35% (14-45%) for both stages between birth and 2 yr of age.

Figure 2 shows a statistically significant association between the ocean and land survival estimates ($r = 0.67$, $P<0.01$). Conditions of weather, feeding, and disease which promote good survival of pups on land apparently equip them to survive relatively well at sea. As in Figure 1, however, the wide scatter about regression is prominent—emphasizing again that events at sea contribute

heavily to fluctuations in the survival of different year classes.

Values in Tables 1 and 2 were also analyzed under the multiple linear regression model

$$Y = A + B_1X_1 + B_2X_2 + B_3X_3 + E$$

where Y = kill at age 3 yr in thousands, X_1 = male pups born in thousands, X_2 = survival rate pups on land, and X_3 = survival rate during the first 20 mo at sea. E is a random error term; the intercept A and slopes B_i are parameters to be estimated.

Table 3 shows that multiple regression is highly significant ($F = 26.60, P<0.001$). Given that the pup survival rate on land is not significant (deletion of X_2 causes no change in R^2 here), 100 R^2 = 82% of the annual variation in estimated abundance at age 3 yr, as indexed by the kill, is explained by annual changes in pup production and in the survival rates of different year classes during their first 20 mo at sea. The remaining variability, 18%, is due to random sampling errors and possibly to systematic errors.

Discussion

This report helps to quantify the importance of early ocean mortality in determining the average number of males available for harvest at age 3 yr and their pronounced annual fluctuations. Kenyon et al. (1954) speculated that only half the pups survive the attempted transition from a milk diet on the Pribilof Islands to the quest for fishes and squids in a stormy environment after the islands are left behind. The authors stated that starvation during prolonged storms is a direct cause of death and noted that unusually large numbers of young seals from the 1949 year class were washed ashore on the Washington coast in emaciated condition during the severe winter of 1949-50. Ichihara (1974) postulated that the apparently higher mortality of males between birth and age 3 yr (Chapman 1964) was due to the greater proportion of males wintering in stormy northern areas than in calmer waters to the south where females predominate.

TABLE 3.—Statistics and tests for linear regression of male seals killed on St. Paul Island at age 3 yr (thousands) from the 1950-70 year classes (Y) on pups born (X_1, thousands), estimated survival rate of pups on land (X_2), and estimated survival rate during the first 20 mo at sea until age 2 yr (X_3).

Item	Calculated value
Source of sum of squares, degrees of freedom, and mean square:	
Multiple regression	1,531.60/3 = 510.53
Deviations	326.26/17 = 19.19
Total	1,857.86/20 = 92.89
Test of multiple regression	F = 510.53/19.19 = 26.60**
Square of multiple correlation	R^2 = 1,531.60/1,857.86 = 0.82
Parameter estimates and variances:	
a, s^2_a	−70.355, 533.294
$b_1, s^2_{b_1}$	0.203, 0.001
$b_2, s^2_{b_2}$	21.389, 753.857
$b_3, s^2_{b_3}$	103.012, 350.151
Tests of individual regresions	
Pups born:	$t_1 = 0.203/\sqrt{0.001} = 6.42$**
Land survival rate	$t_2 = 21.389/\sqrt{753.857} = 0.78$
Ocean survival rate	$t_3 = 103.012/\sqrt{350.157} = 5.50$**

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